# Monitoring and prediction of phytoplankton dynamics in the North Sea

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# References

Aarninkhof, S.G.J., Turner, I.L., Dronkers, T.D.T., Caljouw, M., Nipius, L., 2003. A video-based technique for mapping intertidal beach bathymetry. Coastal Engineering 49: 275-289.

Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanography & Marine Biology - Annual Review 45: 345-405.

Alldredge, A.L., Gotschalk, C.G., 1989. Direct observations of the mass flocculation of diatom blooms: characteristics, settling velocities and formation of diatom aggregates. Deep Sea Research 36: 159-171.

Andersen, V., Prieur, L., 2000. One-month study in the open NW Mediterranean Sea (DYNAPROC experiment, May 1995): overview of the hydrobiogeochemical structures and effects of wind events. Deep-Sea Research I 47: 397-422.

Anderson, D.M., Glibert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. Estuaries 25: 704-726.

Anning, T., MacIntyre, H.L., Pratt, S.M., Sammes, P.J., Gibb, S., Geider, R.J., 2000. Photoacclimation in the marine diatom *Skeletonema costatum*. Limnology and Oceanography 45: 1807-1817.

Antaja, E., Chrétiennot-Dinet, M-J., Leblanc, C., Daro, M-H., Lancelot, C., 2004. 19'-Hexanoyloxyfucoxanthin may not be the appropriate pigment to trace occurrence and fate of *Phaeocystis*: the case of *P. globosa* in Belgian coastal waters. Journal of Sea Research 52: 165-177.

Antia, N.J., Harrison, P.J., Oliveira, L., 1991. The role of dissolved organic nitrogen in phytoplankton nutrition, cell biology and ecology. Phycologia 30: 1-89.

Astoreca, R., Rousseau, V., Ruddick, K., Knechciak, C., Van Mol, B., Parent, J-Y., Lancelot, C., 2009. Development and application of an algorithm for detecting *Phaeocystis globosa* blooms in the Case 2 Southern North Sea waters. Journal of Plankton Research 31: 287-300.

Babin, M., Stramski, D., Ferrari, G.M., Claustre, H., Bricaud, A., Obolensky, G., Hoepffner, N., 2003. Variations in the light absorption coefficients of phytoplankton, nonalgal particles, and dissolved organic matter in coastal waters around Europe. Journal of Geophysical Research 108: 3211-3231.

Balch, W.M., 1981. An apparent lunar tidal cycle of phytoplankton blooming and community succession in the Gulf of Maine. Journal of Experimental Marine Biology and Ecology 55: 65-77.

Baretta, J.W., Ebenhöh, W., Ruardij, P., 1995. The European regional seas ecosystem model, a complex marine ecosystem model. Netherlands Journal of Sea Research 33: 233-246.

Baretta-Bekker, J.G., Baretta, J.W., Latuhihin, M.J., Desmit, X., Prins, T.C., 2009. Description of the long-term (1991-2005) temporal and spatial distribution of phytoplankton carbon biomass in the Dutch North Sea. Journal of Sea Research 61: 50-59.

Baretta-Bekker, J.G., Baretta, J.W., Latuhihin, M.J., Desmit, X., Prins, T.C., 2009. Description of the long-term (1991–2005) temporal and spatial distribution of phytoplankton carbon biomass in the Dutch North Sea, Journal of Sea Research 61: 50-59.

Bätje, M., Michaelis, H., 1986. *Phaeocystis pouchetii* blooms in the East Frisian coastal waters (German Bight, North Sea). Marine Biology 93: 21-27.

Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. Progress in Oceanography 60: 245-262.

Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296: 1692-1694.

Belgrano, A., Lindahl, O., Hernroth, B., 1999. North Atlantic Oscillation primary productivity and toxic phytoplankton in the Gullmar Fjord, Sweden (1985 – 1996). Proceedings of the Royal Society of London B: Biological Sciences 266: 425-430.

Benincà E., Huisman J., Heerkloss R., Jöhnk K.D., Branco P., et al., 2008. Chaos in a long-term experiment with a plankton community. Nature 451: 822-825.

Benincà, E., Dakos, V., Van Nes, E.H., Huisman, J., Scheffer, M., 2011. Resonance of plankton communities with temperature fluctuations. American Naturalist 178: E85-E95.

Beukema, J.J., Baretta-Bakker, J.G., Cadée, G.C., Dronkers, J., Nienhuis, P.H., et al., 1995. European Regional Seas Ecosystem Model I. Netherlands Journal of Sea Research 33: 3-4.

Bjørnstad, O.N., Grenfell, B.T., 2001. Noisy clockwork: time series analysis of population fluctuations in animals. Science 293: 638-643.

Blauw, A.N., Anderson, P., Estrada, M., Johansen, M., Laanemets, J., et al., 2006. The use of fuzzy logic for data analysis and modelling of European harmful algal blooms: results of the HABES project. African Journal of Marine Science 28: 365-369.

Blauw, A.N., Benincà, E., Laane, R.W.P.M., Greenwood, N., Huisman, J., 2012. Dancing with the tides: fluctuations of coastal phytoplankton orchestrated by different oscillatory modes of the tidal cycle. PLoS ONE 7(11): e49319.

Blauw, A.N., Los, F.J., 2004. Analysis of the response of phytoplankton indicators in Dutch coastal waters to nutrient reduction scenarios. WL | Delft Hydraulics, technical report Z3844, December 2004, 145 pp.

Blauw, A.N., Los, F.J., Huisman, J., Peperzak, L., 2010. Nuisance foam events and *Phaeocystis globosa* blooms in Dutch coastal waters analyzed with fuzzy logic. Journal of Marine Systems 83: 115-126.

Blauw, A.N., Los, H.F.J., Bokhorst, M., Erftemeijer, P.L.A., 2009. GEM: a generic ecological model for estuaries and coastal waters. Hydrobiologia 618: 175-198.

Boalch, G.T., 1987. Recent blooms in the Western English Channel. Rapports et procès-verbaux des réunions / Conseil permanent international pour l'exploration de la mer. 187: 94-97.

Boon A.R., Duineveld G.C.A., Berghuis E.M., van der Weele J.A., 1996. Phytopigments and fatty acids as molecular markers for the quality of near-bottom particulate organic matter in the North Sea. Journal of Sea Research 35: 279-291.

Boon, J.G., Desmit X., Blaas, M., 2006. Ecological model of the Lagoon of Venice. Part II: Set-up, calibration and validation. WL | Delft Hydraulics, technical report Z3733, May 2006, 232 pp.

Bot, P.V., Colijn, F., 1996. A method for estimating primary production from chlorophyll concentrations with results showing trends in the Irish Sea and the Dutch coastal zone. ICES Journal of Marine Science: Journal du Conseil 53 : 945-950.

Brauer, V.S., Stomp, M., Huisman, J., 2012. The nutrient-load hypothesis: patterns of resource limitation and community structure driven by competition for nutrients and light. American Naturalist 179: 721-740.

Bresnan, E., Hay, S., Hughes, S.L., Fraser, S., Rasmussen, J., et al., 2009. Seasonal and interannual variation in the phytoplankton community in the north east of Scotland. Journal of Sea Research 61: 17-25.

Breton, E., Rousseau, V., Parent, J.Y., Ozer, J., Lancelot, C., 2006. Hydroclimatic modulation of diatom/ *Phaeocystis* blooms in nutrient-enriched Belgian coastal waters (North Sea). Limnology and Oceanography 51: 1401-1409.

Brinkman, A.G., 1993. Biological processes in the Ecowasp ecosystem model. Institute for Forestry and Nature Research (IBN-DLO), IBN research report 93/6, ISSN: 0928-6896.

Brown, C.J., Schoeman, D.S., Sydeman, W.J., Brander, K., Buckley, L.B., et al., 2011. Quantitative approaches in climate change ecology. Global Change Biology 17: 3697-3713.

Brown, J., Fernand, L., Horseburgh, K.J., Hill, A.E., Read, J.W., 2001. Paralytic shellfish poisoning on the east coast of the UK in relation to seasonal density-driven circulation. Journal of Plankton Research 23: 105-116.

Brunet, C., Casotti, R., Vantrepotte, V., 2008. Phytoplankton diel and vertical variability in photobiological responses at a coastal station in the Mediterranean Sea. Journal of Plankton Research 30: 645-654.

Brunet, C., Lizon, F., 2003. Tidal and diel periodicities of size-fractionated phytoplankton pigment signatures at an offshore station in the southeastern English Channel. Estuarine and Coastal Shelf Science 56: 833-843.

Brussaard, C.P.D., Kuipers, B., Veldhuis, M.J.W., 2005. A mesocosm study of *Phaeocystis globosa* population dynamics - Regulatory role of viruses in bloom. Harmful Algae 4: 859-874.

Burd, A.B., Jackson, G.A., 2009. Particle aggregation. Annual Review of Marine Science 1: 65-90.

Burson, A., Matthijs, H.C.P., de Bruijne, W., Talens, R., Hoogenboom, R., et al., 2014. Termination of a toxic *Alexandrium* bloom with hydrogen peroxide. Harmful Algae 31: 125-135.

Cadée, G.C., Hegeman, J., 1986. Seasonal and annual variation in *Phaeocystis pouchetii* (Haptophyceae) in the westernmost inlet of the Wadden Sea during the 1973 to 1985 period. Netherlands Journal of Sea Research 20: 29-36.

Cadée, G.C., Hegeman, J., 2002. Phytoplankton in the Marsdiep at the end of the 20th century; 30 years monitoring biomass, primary production and *Phaeocystis* blooms. Journal of Sea Research 48: 97-110.

Calbet, A., Vaqué, D., Felipe, J., Vila, M., Sala, M.M., et al., 2003. Relative grazing impact of microzooplankton and mesozooplankton on a bloom of the toxic dinoflagellate *Alexandrium minutum*. Marine Ecology Progress Series 259: 303-309.

Callaway, R., Engelhard, G.H., Dann, J., Cotter, J., Rumohr, H., 2007. One century of North Sea epibenthos and fishing: comparison between 1902-1912, 1982-1985 and 2000. Marine Ecology Progress Series 346: 27-43.

Capuzzo, E., Painting, S.J., Forster, R.M., Greenwood, N., Stephens, D.T., et al., 2013. Variability in the sub-surface light climate at ecohydrodynamically distinct sites in the North Sea. Biogeochemistry 113: 85-103.

Cariou, V., Casotti, R., Birrien, J., Vaulot, D., 1994. The initiation of *Phaeocystis* colonies. Journal of Plankton Research 16: 457-470.

Carvalho, W.F., Minnhagen, S., Granéli, E., 2008. *Dinophysis norvegica* (Dinophyceae), more a predator than a producer? Harmful Algae 7: 174-183.

Cazelles, B., Chavez, M., Berteaux, D., Ménard, F., Vik, J.O., et al., 2008. Wavelet analysis of ecological time series. Oecologia 156: 287-304.

Chatfield, C., 2013. The analysis of time series: an introduction. CRC Press, Boca Raton, USA.

Chen, Z., Hu, C., Muller-Karger, F.E., Luther, M.E., 2010. Short-term variability of suspended sediment and phytoplankton in Tampa Bay, Florida: observations from a coastal oceanographic tower and ocean color satellites. Estuarine and Coastal Shelf Science 89: 62-72.

Cloern, J.E., 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. Continental Shelf Research 7: 1367-1381.

Cloern, J.E., Jassby, A., 2010. Patterns and scales of phytoplankton variability in estuarine–coastal ecosystems. Estuaries and Coasts 33: 230–241, doi:10.1007/s12237-009-9195-3

Cloern, J.E.1991. Tidal stirring and phytoplankton bloom dynamics in an estuary. Journal of Marine Research 49: 203-221.

Colijn, F., Cadée, G.C., 2003. Is phytoplankton growth in the Wadden Sea light or nitrogen limited? Journal of Sea Research 49: 83-93.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

Culverhouse, P.F., Williams, R., Reguera, B., Herry, V., González-Gil, S., 2003. Do experts make mistakes? A comparison of human and machine identification of dinoflagellates. Marine Ecology Progress Series 247: 17-25.

D'Sa, E.J., Miller, R.L., 2005. Bio-optical properties of coastal waters, in Remote Sensing of Coastal Aquatic Environments, R.L. Miller, C.E. del Castillo and B.A. McKee (eds.), Springer, Dordrecht, The Netherlands, ISBN 1-4020-3099-1, pp. 129-155.

Dahl, E., Johannessen, T., 1998. Temporal and spatial variability of phytoplankton and chlorophyll a: lessons from the south coast of Norway and the Skagerrak. ICES Journal of Marine Science: Journal du Conseil 55: 680-687.

Dakos, V., Benincà, E., van Nes, E.H., Philippart, C.J., Scheffer, M., et al., 2009. Interannual variability in species composition explained as seasonally entrained chaos. Proceedings of the Royal Society B: Biological Sciences 276: 2871-2880.

Danzig, G.B., 1963. Linear programming and extensions. Princeton University Press, Princeton, N.J.

De Boer, G.J., Pietrzak, J.D., Winterwerp, J.C., 2009. SST observations of upwelling induced by tidal straining in the Rhine ROFI. Continental Shelf Research 29: 263-277.

De Brouwer, J.F.C., Bjelic, S., de Deckere, E.M.G.T., Stal, L.J., 2000. Interplay between biology and sedimentology in a mudflat (Biezelingse Ham, Westerschelde, The Netherlands). Continental Shelf Research 20: 1159-1177.

De Jonge, V.N., Van Beusekom, J.E.E., 1995. Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. Limnology and Oceanography 40: 766-778.

De Kok, J.M., de Valk, C., Van Kester, J.H.T.M., de Goede, E., Uittenbogaard, R.E., 2001. Salinity and temperature stratification in the Rhine plume. Estuarine, Coastal and Shelf Science 53: 467-475.

De Kok, J.M., Salden, R., Roozendaal, I.D.M., Blokland, P., Lander, J., 1995. Transport paths of suspended matter along the Dutch coast. In: Brebbia, C.A., L. Traversoni & L.C. Wrobel (eds), Computer Modelling of Seas and Coastal Regions II. Computational Mechanics Publications, Southampton: 75-86.

De Ruijter, W.P.M., Visser, A.W., Bos, W.G., 1997. The Rhine outflow: a prototypical pulsed discharge plume in a high energy shallow sea. Journal of Marine Systems 12: 263-276.

De Vries, I., Duin, R.N.D., Peeters, J.C.H., Los, F.J., Bokhorst, M., Laane, R.W.P.M., 1998. Patterns and trends in nutrients and phytoplankton in Dutch coastal waters: comparison of time-series analysis, ecological model simulation and mesocosm experiments. ICES Journal of Marine Science 55: 620-634.

Delhez, E.J.M., Damm, P., De Goede, E.D., De Kok, J.M., Dumas, F., et al., 2004. Variability of shelf-seas hydrodynamic models: lessons from the NOMADS2 project. Journal of Marine Systems 45: 39-53.

Denman K.J., Gargett A.E., 1995. Biological-physical interactions in the upper ocean: the role of vertical and small scale transport processes. Annual Review of Fluid Mechanics 27: 225-256.

Devlin, M, Best, M., Haynes, D., 2007. Implementation of the Water Framework Directive in European marine waters. Marine Pollution Bulletin 55: 1-2.

Dickey, T., Zedler, S., Yu, X., Doney, S.C., Frye, D., et al., 2001. Physical and biogeochemical variability from hours to years at the Bermuda Testbed Mooring site: June 1994-March 1998. Deep-Sea Research II 48: 2105-2140.

Droesen, W.J., 1996. Formalisation of ecohydrological expert knowledge applying fuzzy techniques. Ecological Modelling 85: 75-82.

Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmüller, V., Dye, S.R., Skjoldal, H.R., 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology 45: 1029-1039.

Dyhrman, S.T., Anderson, D.M., 2003. Urease activity in cultures and field populations of the toxic dinoflagellate *Alexandrium*. Limnology and Oceanography 48: 647-655.

Edwards, K.P., Barciela, R., Butenschön, M., 2012. Validation of the NEMO-ERSEM operational ecosystem model for the North West European Continental Shelf. Ocean Science 8: 983-1000.

Edwards, M., Beaugrand, G., Helaouët, P., Alheit, J., Coombs, S., 2013. Marine ecosystem response to the Atlantic Multidecadal Oscillation. PLoS ONE 8(2): e57212, doi:10.1371/journal.pone.0057212

Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430: 881-884.

Elton, C.S., 1924. Periodic fluctuations in the numbers of animals: their causes and effects. British Journal of Experimental Biology 2: 119-163.

Estrada, M., Arin, L., Blasco, D., Blauw, A., Camp, J., Garces, E., Sampedro, N., Vila, M.., 2008. A fuzzy logic model for *Alexandrium minutum* proliferations in harbours of the Catalan coast (NW Mediterranean). Proceedings of the XI th conference on Harmful Algal Blooms, Copenhagen 2006.

Fitz, H.C., DeBellevue, E.B., Costanza, R., Boumans, R., Maxwell, T., et al.,, 1996. Development of a general ecosystem model for a range of scales and ecosystems. Ecological Modelling 88: 263-295.

Flöder, S., Sommer, U., 1999. Diversity in planktonic communities: an experimental test of the intermediate disturbance hypothesis. Limnology and Oceanography 44: 1114-1119.

Franks, J.P.S. 1997. Models of harmful algal blooms. Limnology and Oceanography 42: 1273-1282.

Franks, P.J.S., 2005. Plankton patchiness, turbulent transport and spatial spectra. Marine Ecology Progress Series 294: 295-309.

Fussmann, G.F., Ellner, S.P., Shertzer, K.W., Hairston, N.G. Jr., 2000. Crossing the Hopf bifurcation in a live predator-prey system. Science 290: 1358-1360.

Gaedeke, A., Sommer, U., 1986. The influence of the frequency of periodic disturbances on the maintenance of phytoplankton diversity. Oecologia 71: 25-28.

Gause, G.F., 1934. The struggle for existence. Williams & Wilkins, Baltimore.

Geider, R.J., 1987. Light and temperature dependence of the carbon to chlorophyll a ratio in microalgae and cyanobacteria: implications for physiology and growth of phytoplankton. New Phytologist 106: 1-34.

Gerritsen, H., Boon, J.G., Van der Kaaij, T., Vos, R.J., 2001. Integrated modelling of suspended matter in the North Sea. Estuarine, Coastal & Shelf Science 53: 581-594.

Gieskes, W.W.C., Leterme, S.C., Peletier, H., Edwards, M., Reid, P.C., 2007. *Phaeocystis* colony distribution in the North Atlantic Ocean since 1948, and interpretation of long-term changes in the *Phaeocystis* hotspot in the North Sea. Biogeochemistry 83: 49-60.

Godhe, A., Svensson, S., Rehnstam-Holm, A., 2002. Oceanographic settings explain fluctuations in *Dinophysis* spp. and concentrations of diarrhetic shellfish toxin in the plankton community within a mussel farm area on the Swedish west coast. Marine Ecology Progress Series 240: 71-83.

Gonzalez, N.E., Muller-Karger, F.E., Estrada, S.C., de los Reyes, R.P., del Rio, I.V. et al., 2000. Near-surface phytoplankton distribution in the western Intra-Americas Sea: the influence of El Nino and weather events. Journal of Geophysical Research 105: 14029-14043.

Greenfield, D.I., Marin III, R., Doucette, G.J., Mikulski, C., Jones, K., et al., 2008. Field applications of the second-generation Environmental Sample Processor (ESP) for remote detection of harmful algae. Limnology and Oceanography: Methods 6: 667-679.

Greenwood, N., Parker, E.R., Fernand, L., Sivyer, D.B., Weston, K., et al., 2010. Detection of low bottom water oxygen concentrations in the North Sea; implications for monitoring and assessment of ecosystem health. Biogeosciences 7: 1357-1373.

Gregg, W.W., 2008. Assimilation of SeaWiFS ocean chlorophyll data into a three-dimensional global ocean model. Journal of Marine Systems, 69: 205-225.

Grinsted, A., Moore, J.C., Jevrejeva, S., 2004. Application of the cross wavelet transform and wavelet coherence to geophysical time series. Nonlinear Processes in Geophysics 11: 561-566.

Grover, J.P. 1991. Resource competition in a variable environment: phytoplankton growing according to the variable-internal-stores model. American Naturalist 136: 811-835.

Gypens, N., Lacroix, G., Lancelot, C. 2007. Causes of variability in diatom and *Phaeocystis* blooms in Belgian coastal waters between 1989 and 2003: A model study. Journal of Sea Research 57: 19-35.

Hallegraeff, G.M., 1993. A review of harmful algal blooms and their apparent global increase. Phycologia 32: 79-99.

Hamm, C.E., Rousseau, V., 2003. Composition, assimilation and degradation of *Phaeocystis globosa*-derived fatty acids in the North Sea. Journal of Sea Research 50: 271-283.

Hansen, G., Daugbjerg, N., Franco, J.M., 2003. Morphology, toxin composition and LSU rDNA phylogeny of *Alexandrium minutum* (Dinophyceae) from Denmark, with some morphological observations on other European strains. Harmful Algae 2: 317-335.

Harris, G.P., 1980. Temporal and spatial scales in phytoplankton ecology: mechanisms, methods, models, and management. Canadian Journal of Fisheries and Aquatic Sciences 37: 877-900.

Harris, G.P., 1986. Phytoplankton ecology. Chapman and Hall, London.

Harris, R., 2010. The L4 time-series: the first 20 years. Journal of Plankton Research 32: 577-583.

Hastie, T., Tibshirani, R.J., 1990. Generalized additive models. London, UK: Chapman & Hall.

Hesselmans, G.H.F.M., Blauw, A.N., Tatman, S., 2005. Algae bloom warning service. Geomatics Business Park, rapport: RP_A360

Huisman, J., Jonker, R.R., Zonneveld, C., Weissing, F.J., 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. Ecology 80: 211-222.

Huisman, J., Pham Thi, N.N., Karl, D.M., Sommeijer, B., 2006. Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum. Nature 439: 322-325.

Huisman, J., Sharples, J., Stroom, J., Visser, P.M., Kardinaal, W.E.A., et al., 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology 85: 2960-2970.

Huisman, J., Sommeijer, B., 2002. Maximal sustainable sinking velocity of phytoplankton. Marine Ecology Progress Series 244: 39-48.

Huisman, J., van Oostveen P., Weissing, F.J., 1999. Critical depth and critical turbulence: two different mechanisms for the development of phytoplankton blooms. Limnology and Oceanography 44: 1781-1787.

Huisman, J., Weissing, F.J., 1994. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. Ecology 75: 507-520.

Huisman, J., Weissing, F.J., 1999. Biodiversity of plankton by species oscillations and chaos. Nature 402: 407-410.

Huppert, A., Blasius, B., Stone, L. 2002. A model of phytoplankton blooms. American Naturalist 159: 156-171.

Huret, M., Gohin, F., Delmas, D., Lunven, M., Garçon, V., 2007. Use of SeaWiFS data for light availability and parameters estimation of a phytoplankton production model of the Bay of Biscay. Journal of Marine Systems 65: 509-531.

Hutchinson, G.E., 1961. The paradox of the plankton. American Naturalist 95: 137-145.

Ibelings, B.W., Vonk, M., Los, H.F.J., Van der Molen, D.T., Mooij, W.M., 2003. Fuzzy modelling of cyanobacterial surface waterblooms: validation with NOAA-AVHRR satellite images. Ecological Applications 13: 1456-1472.

Jago, C.F., Jones, S.E., 1998. Observation and modelling of the dynamics of benthic fluff resuspended from a sandy bed in the southern North Sea. Continental Shelf Research 18: 1255-1282.

Jahnke, J., 1989. The light and temperature dependence of growth rate and elemental composition of *Phaeocystis globosa* Scherffel and *P. pouchetii* (Har.) Lagerh. in batch cultures. Netherlands Journal of Sea Research 23: 15-21.

Jakob, T., Schreiber, U., Kirchesch, V., Langner, U., Wilhelm, C., 2005. Estimation of chlorophyll content and daily primary production of the major algal groups by means of multiwavelength-excitation PAM chlorophyll fluorometry: performance and methodological limits. Photosynthesis Research 83: 343-361.

Jiang, S., Dickey, T.D., Steinberg, D.K., Madin, L.P., 2007. Temporal variability of zooplankton biomass from ADCP backscatter time series data at the Bermuda Testbed Mooring site. Deep-Sea Research I 54: 608–636, doi: 10.1016/j.dsr.2006.12.011

Joordens, J.C.A., Souza, A.J., Visser, A., 2001. The influence of tidal straining and wind on suspended matter and phytoplankton distribution in the Rhine outflow region. Continental Shelf Research 21: 301-325.

Kernkamp, H., Boot G., Nolte A., 2002. Onderzoek naar de toekomstige waterkwaliteit en ecologie van het Veerse Meer. Studie naar het effect van het doorlaatmiddel en aanvullende maatregelen. Deel 1: Opzet en kalibratie hydrodynamisch en waterkwaliteitsmodel. WL | Delft Hydraulics, technical report Z3304, November 2002, 81 pp.

Kiefer, D.A., 1973. Fluorescence properties of natural phytoplankton populations. Marine Biology 22: 263-269.

Kiefer, D.A., 1973. Fluorescence properties of natural phytoplankton populations. Marine Biology22: 263-269.

Kirk, J.T.O., 1994. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge.

Klein Tank, A.M.G., Wijngaard, J.B., Können, G.P., Böhm, R., Demarée, G., et al., 2002. Daily dataset of 20th-century surface air temperature and precipitation series for the European Climate Assessment. International Journal of Climatology 22: 1441-1453.

Klein, A.W.O., van Buuren, J.T., 1992. Eutrophication of the North Sea in the Dutch coastal zone 1976-1990. Tidal Waters Division, report: DGW-92.003. (available at: http://publicaties.minienm.nl/documenten/)

Klepper, O., Van der Tol, W.M., Scholten, H., Herman, P.M.J., 1994. SMOES: a simulation model for the Oosterschelde ecosystem. Part 1: Description and uncertainty analysis. Hydrobiologia 282/283: 453-474.

Koelle, K., Pascual, M., 2004. Disentangling extrinsic from intrinsic factors in disease dynamics: a nonlinear time series approach with an application to cholera. American Naturalist 163: 901-913.

Kolmogorov, A.N., 1941. The local structure of turbulence in an incompressible viscous fluid for very large Reynolds number. Comptes Rendus de l'Académie des Sciences USSR 30: 301-305.

Kornmann, P., 1955. Beobachtungen an Phaeocystis-Kulturen. Helgoländer Wissenschaftliche Meeresuntersuchungen 5: 218-233.

Kraberg, A.C., Wasmund, N., Vanaverbeke, J., Schiedek, D., Wiltshire, K.H., et al., 2011. Regime shifts in the marine environment: the scientific basis and political context. Marine Pollution Bulletin 62: 7-20.

Kröger, S., Parker, E.R., Metcalfe, J.D., Greenwood, N., Forster, R.M., et al., 2009. Sensors for observing ecosystem status. Ocean Science 5: 523-535.

Kurekin, A.A., Miller, P.I., Van Der Woerd, H.J., 2014. Satellite discrimination of *Karenia mikimotoi* and *Phaeocystis* harmful algal blooms in European coastal waters: merged classification of ocean colour data. Harmful Algae 31: 163-176.

Laane, R.W.P.M., Southward, A.J., Slinn, D.J., Allen, J., Groeneveld, G., et al., 1996. Changes and causes of variability in salinity and dissolved inorganic phosphate in the Irish Sea, English Channel, and Dutch coastal zone. ICES Journal of Marine Science: Journal du Conseil 53 : 933-944.

Laanemets, J., Lilover, M.J., Raudsepp, U., Autio, R., Vahtera, E., Lips, I., Lips, U., 2006. A fuzzy logic model to describe the cyanobacteria *Nodularia spumigena* blooms in the Gulf of Finland, Baltic Sea. Hydrobiologia 554: 31-45.

Lacroix, G., Ruddick, K., Ozer, J., Lancelot, C., 2004. Modelling the impact of the Scheldt and Rhine/Meuse plumes on the salinity distribution in Belgian waters (southern North Sea). Journal of Sea Research 52: 149-163.

Lacroix, G., Ruddick, K., Park, Y., Gypens, N., Lancelot, C., 2007. Validation of the 3D biogeochemical model MIRO&CO with field nutrient and phytoplankton data and MERIS-derived surface chlorophyll a images. Journal of Marine Systems 64: 66-88.

Lancelot, C., Spitz, Y., Gypens, N. , Ruddick, K., Becquevort, S., Rousseau, V., Lacroix, G., Billen, G., 2005. Modelling diatom and *Phaeocystis* blooms and nutrient cycles in the Southern Bight of the North Sea: the MIRO model. Marine Ecology Progress Series 289: 63-78.

Lancelot, C., 1995. The mucilage phenomenon in the continental coastal waters of the North Sea. Science of the Total Environment 165: 83-102.

Lancelot, C., Keller, M.D., Rousseau, V., Smith, W.O., Jr., Mathot, S., 1998. Autecology of the marine haptophyte *Phaeocystis* sp. In: D.M.Anderson, A.D.Cembella, G.M.Hallegraeff (eds) Physiological ecology of harmful algal blooms. Springer Berlin, pp. 209-224.

Lancelot, C., Rousseau, V., Billen, G., Van Eeckhout, D., 1997. Coastal eutrophication of the southern bight of the North Sea: assessment and modelling. In: Özsoy E, Mikaelyan A (eds) Sensitivity to Change: Black Sea, Baltic Sea and North Sea. Kluwer Academic Publishers, Netherlands, pp. 439-453.

Lancelot, C., Rousseau, V., Gypens, N., 2009. Ecologically based indicators for *Phaeocystis* disturbance in eutrophied Belgian coastal waters (Southern North Sea) based on field observations and ecological modelling. Journal of Sea Research 61: 44-49.

Lancelot, C., Spitz, Y., Gypens, N., Ruddick, K., Becquevort, S., et al., 2005. Modelling diatom and *Phaeocystis* blooms and nutrient cycles in the Southern Bight of the North Sea: the MIRO model. Marine Ecology Progress Series 289: 63-78.

Lane, J.Q., Raimondi, P.T., Kudela, R.M., 2009. Development of a logistic regression model for the prediction of toxigenic *Pseudo-nitzschia* blooms in Monterey Bay, California. Marine Ecology Progress Series 383: 37-51.

Lauria, M.L., Purdie, D.A., Sharples, J., 1999. Contrasting phytoplankton distributions controlled by tidal turbulence in an estuary. Journal of Marine Systems 21: 189-197.

Lekve, K., Enersen, K., Enersen, S.E., Gjøsæter, J., Stenseth, N.C., 2006. Interannual variability in abundance and length of young coastal cod in the subtidal zone. Journal of Fish Biology 68: 734-746.

Li, H., Arias, M., Blauw, A., Los, H., Mynett, A.E., Peters, S., 2010. Enhancing generic ecological model for short-term prediction of Southern North Sea algal dynamics with remote sensing images. Ecological Modeling 221: 2435-2446.

Lilover, M.J. , Laanemets, J., 2003. Impact of turbulent nutrient fluxes on the late summer cyanobacterial bloom. Geophysical Research Abstracts 5 EGS-AGU-EUG Joint Assembly.

Lilover, M.J., Laanemets, J., 2006. A simple tool for the early prediction of the cyanobacteria *Nodularia spumigena* bloom biomass in the Gulf of Finland. Oceanologia 48: 213-229.

Lilover, M.J., Laanemets, J., Kullas, T., Stips, A., Kononen, K., 2003. Late summer vertical nutrient fluxes estimated from direct turbulence measurements: Gulf of Finland case study. Proceedings of the Estonian Academy of Sciences, Ecology 3: 193-204.

Lindeboom, H.J., 1995. Protected areas in the North Sea: an absolute need for future marine research. Helgoländer Meeresuntersuchungen 49: 591-602.

Liss, P.S., Malin, G., Turner, S.M., Holligan, P.M., 1994. Dimethyl sulphide and Phaeocystis: A review. Journal of Marine Systems 5: 41-53.

Llope, M., Chan, K.S., Ciannelli, L., Reid, P.C., Stige, L.C., et al., 2009. Effects of environmental conditions on the seasonal distribution of phytoplankton biomass in the North Sea. Limnology and Oceanography 54: 512-524.

Loebl, M., Colijn, F., van Beusekom, J.E., Baretta-Bekker, J.G., Lancelot, C., et al., 2009. Recent patterns in potential phytoplankton limitation along the Northwest European continental coast. Journal of sea research 61: 34-43.

Lorenz, E.N., 1963. Deterministic nonperiodic flow. Journal of the Atmospheric Sciences 20: 130-141.

Los, F.J., Blaas, M., 2010. Complexity, accuracy and practical applicability of different biogeochemical model versions. Journal of Marine Systems 81: 44-74.

Los, F.J., Bokhorst, M., 1997. Trend analysis Dutch coastal zone. In: New Challenges for North Sea Research, Zentrum fur Meeres- und Klimaforschung, University of Hamburg: 161-175.

Los, F.J., Brinkman, J.J., 1988. Phytoplankton modelling by means of optimization: a 10-year experience with BLOOM II. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 23: 790-795.

Los, F.J., de Rooij, N.M., Smits, J.G.C., 1984. Modelling eutrophication in shallow Dutch lakes. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22: 917-923.

Los, F.J., Jansen, R., Cramer, S., 1994. MANS Eutrophication Modelling System. National Institute for Coastal and Marine Management / RIKZ, The Hague, 137 pp.

Los, F.J., Villars, M.T., Van der Tol, M.W.M., 2008. A 3-dimensional primary production model (BLOOM/GEM) and its applications to the (southern) North Sea (coupled physical-chemical-ecological model). Journal of Marine Systems 74: 259-294.

Los, F.J., Wijsman, J.W.M., 2007. Application of a validated primary production model (BLOOM) as a screening tool for marine, coastal and transitional waters. Journal of Marine Systems 64: 201-215.

Lotka, A.J., 1925. Elements of Physical Biology. Williams & Wilkins, Baltimore.

Loucks, D.P., Van Beek, E. (eds), 2005. Water Resources Systems Planning and Management - an introduction to methods, models and applications. Chapter 12: 'Water quality modelling and prediction'. Studies and Reports in Hydrology, UNESCO publishing, ISBN 92-3-103998-9.

Lucas, C.H., Widdows, J., Brinsley, M.D., Salkeld, P.N., Herman, P.M.J., 2000. Benthic-pelagic exchange of microalgae at a tidal flat. 1. Pigment analysis. Marine Ecology Progress Series196: 59-73.

MacIntyre, H.L., Geider, R.J., Miller, D.C., 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. Estuaries 19: 186-201.

MacKenzie, B.R., Myers, R.A., 2007. The development of the northern European fishery for north Atlantic bluefin tuna Thunnus thynnus during 1900–1950. Fisheries Research 87: 229-239.

Mackey, M.D., Mackey, D.J., Higgins, H.W., Wright, S.W., 1996. CHEMTAX , a program for estimating class abundances from chemical markers: application to HPLC measurements of phytoplankton. Marine Ecology Progress Series 144: 265-283.

Malta, E.J., Verschuure, J.M., 1997. Effects of environmental variables on between-year variation of *Ulva* growth and biomass in a eutrophic brackish lake. Journal of Sea Research 38: 71-84.

Mann, K.H., Lazier, J.R.N., 2009. Dynamics of marine ecosystems: biological-physical interactions in the oceans. Blackwell Publishing Ltd, USA

May, C.L., Koseff, J.R., Lucas, L.V., Cloern, J.E., Schoellhamer, D.H., 2003. Effects of spatial and temporal variability of turbidity on phytoplankton blooms. Marine Ecology Progress Series 254: 111-128.

McCandliss, R.R., Jones, S.E., Hearn, M., Latter, R., Jago, C.F., 2002. Dynamics of suspended particles in coastal waters (southern North Sea) during a spring bloom. Journal of Sea Research 47: 285-302.

McCauley, E., Nisbet, R.M., Murdoch, W.W., De Roos, A.M., Gurney, W.S.C. 1999. Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments. Nature 402: 653-656.

McQuatters-Gollop, A., Vermaat, J.E., 2011. Covariance among North Sea ecosystem state indicators during the past 50 years: contrasts between coastal and open waters. Journal of Sea Research 65: 284-292.

McQuoid, M.R., Nordberg, K., 2003. The diatom *Paralia sulcata* as an environmental indicator species in coastal sediments. Estuarine and Coastal Shelf Science 56: 339-354.

Meyer, T.M., Sacareau, P., 2012. Sensors and monitoring: state of the art and research needs. WssTP report, www.wsstp.eu.

Mills, D.K., Laane, R.W.P.M., Rees, J.M., Rutgers van der Loeff, M., Suylen, J.M., et al., 2003. Smartbuoy: a marine environmental monitoring buoy with a difference. Elsevier Oceanography Series 69: 311-316.

Mobley, C.D., 1994. Light and water; radiative transfer in natural waters, Academic Press, London.

Moll A., Radach G., 2003. Review of three-dimensional ecological modelling related to the North Sea shelf system - Part 1: models and their results. Progress in Oceanography 57: 175-217.

Muylaert, K., Gonzales, R., Franck, M., Lionard, M., Van der Zee, C., Cattrijsse, A., Sabbe, K., Chou, L., Vyverman, W., 2006. Spatial variation in phytoplankton dynamics in the Belgian coastal zone of the North Sea studied by microscopy, HPLC-CHEMTAX and underway fluorescence recordings. Journal of Sea Research 55: 253-265.

Muylaert, K., Sabbe, K., 1999. Spring phytoplankton assemblages in and around the maximum turbidity zone of the estuaries of the Elbe (Germany), the Schelde (Belgium/The Netherlands) and the Gironde (France). Journal of Marine Systems 22: 133-149.

Naustvoll, L.J., Gustad, E., Dahl, E., 2012. Monitoring of *Dinophysis* species and diarrhetic shellfish toxins in Flodevigen Bay, Norway: inter-annual variability over a 25-year time-series. Food Additives Contaminants Part A 29: 1605-1615.

Nechad, B., Alvera-Azcaràte, A., Ruddick, K., Greenwood, N., 2011. Reconstruction of MODIS total suspended matter time series maps by DINEOF and validation with autonomous platform data. Ocean Dynamics 61: 1205-1214.

Niermann, U., Bauerfeind, E., Hickel, W., Westernhagen, H.V., 1990. The recovery of benthos following the impact of low oxygen content in the German Bight. Netherlands Journal of Sea Research 25: 215-226.

Nolte, A., Boderie, P., van Beek, J., 2005. Impacts of Maasvlakte 2 on the Wadden Sea and North Sea coastal zone. Track 1: Detailed modelling research. Part III: Nutrients and Primary Production. WL | Delft Hydraulics, technical report Z3945, November 2005, 175 pp.

Nolte, A., Chua, G., 2003. Evaluation and Future Prospects of the Laguna de Bay Water Quality Model. Technical report for the 'Sustainable Development of the Laguna de Bay Environment' project, WL | Delft Hydraulics, June 2003.

Olsson, P., Granéli, E., 1991. Observations on diurnal migration and phased cell division for three coexisting marine dinoflagellates. Journal of Plankton Research 13: 1313-1324.

OSPAR Commission, 2008. Second OSPAR Integrated Report on the Eutrophication Status of the OSPAR Maritime Area. OSPAR Eutrophication Series, publication 372/2008. OSPAR Commission, London, pp. 107

OSPAR, 1998. Report of the ASMO modelling workshop on eutrophication issues, 5-8 November 1996, The Hague, The Netherlands. OSPAR Commission Report, Netherlands Institute for Coastal and Marine Management / RIKZ, The Hague, The Netherlands.

OSPAR, 2010. The Common Procedure for the Identification of the Eutrophication Status of the OSPAR maritime area. See www.ospar.org. Last access 30 July 2010.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C., Stenseth, N.C., 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128: 1-14, doi: 10.1007/s004420100655

Ouboter, M.R.L., Van Eck, B.T.M., Van Gils, J.A.G., Sweerts, J.P., Villars, M.T., 1998. Water quality modelling of the western Scheldt estuary. Hydrobiologia 366: 129-142.

Padisák, J., Reynolds, C.S., Sommer, U. [eds], 1993. Intermediate disturbance hypothesis in phytoplankton ecology. Developments in Hydrobiology 81, Kluwer Academic Publishers, Dordrecht.

Paerl, H.W., Huisman, J., 2008. Blooms like it hot. Science 320: 57-58.

Park, M.G., Kim, S., Kim, H.S., Myung, G., Kang, Y.G., Yih, W., 2006. First successful culture of the marine dinoflagellate *Dinophysis acuminata*. Aquatic Microbial Ecology 45: 101-106.

Passarge, J., Hol, S., Escher, M., Huisman, J., 2006. Competition for nutrients and light: stable coexistence, alternative stable states, or competitive exclusion? Ecological Monographs 76: 57-72.

Passow, U., 2002. Transparent exopolymer particles (TEP) in aquatic environments. Progress in Oceanography 55: 287-333.

Peperzak, L., 1993. Daily irradiance governs growth rate and colony formation of *Phaeocystis* (Prymnesiophyceae). Journal of Plankton Research 15: 809-821.

Peperzak, L., 2002. The wax and wane of *Phaeocystis globosa* blooms. PhD Thesis. University of Groningen, The Netherlands. (http://dissertations.ub.rug.nl/).

Peperzak, L., 2010. An objective procedure to remove observer-bias from phytoplankton time-series. Journal of Sea Research 63: 152-156.

Peperzak, L., Colijn, F., Gieskes, W.W.C., Peeters, J.C.H., 1998. Development of the diatom-*Phaeocystis* spring bloom in the Dutch coastal zone (North Sea): the silicon depletion versus the daily irradiance hypothesis. Journal of Plankton Research 20: 517-537.

Peperzak, L., Poelman, M., 2008. Mass mussel mortalitly in the Netherlands after a bloom of *Phaeocystis globosa* (prymnesiophyceae). Journal of Sea Research 60: 220-222.

Peters, S.W.M., Eleveld, M., Pasterkamp, R., Van der Woerd, H., Devolder, M., et al., 2005. Atlas of chlorophyll-a concentration for the North Sea based on MERIS imagery of 2003. Free University of Amsterdam.

Peters, S.W.M., Van der Woerd, H.J., Eleveld, M.A., 2009. Validation of the MERIS water-quality information in the Dutch EEZ for the years 2003-2006. The Ovatie report. IVM – report, Amsterdam, The Netherlands.

Petersen, W., Wehde, H., Krasemann, H., Colijn, F., Schroeder, F., 2008. FerryBox and MERIS assessment of coastal and shelf sea ecosystems by combining in situ and remotely sensed data. Estuarine, Coastal and Shelf Science 77: 296-307.

Philippart, C.J.M., van Iperen, J.M., Cadée, G.C., Zuur, A.F., 2010. Long-term field observations on seasonality in chlorophyll-a concentrations in a shallow coastal marine ecosystem, the Wadden Sea. Estuaries and coasts 33: 286-294.

Pietrzak, J.D., De Boer, G.J., Eleveld, M.A., 2011. Mechanisms controlling the intra-annual mesoscale variability of SST and SPM in the southern North Sea. Continental Shelf Research 31: 594-61.

Pomati, F., Jokela, J., Simona, M., Veronesi, M., Ibelings, B.W., 2011. An automated platform for phytoplankton ecology and aquatic ecosystem monitoring. Environmental Science Technology 45: 9658-9665.

Prins, T.C., Smaal, A.C., Dame, R.F., 1997. A review of the feedbacks between bivalve grazing and ecosystem processes. Aquatic Ecology 31: 349-359.

Pugh, D.T., 1996. Tides, Surges and Mean Sea-Level. Chichester: John Wiley & Sons. 472 pp.

Purdie, D., Holeton, C., Iriarte, A., 2004. Pilot study English coastal waters. In: Blauw AN (ed) Harmful Algal Blooms Expert System, final report. Delft Hydraulics, pp. 5-1 - 5-79 http://habes.hrwallingford.co.uk/.

Radach, G., Gekeler, J., 1996. Annual cycles of horizontal distributions of temperature and salinity, and of concentrations of nutrients, suspended particulate matter and chlorophyll on the northwest European shelf. Deutsche Hydrografische Zeitschrift 48: 261-297.

Radach, G., Moll, A., 2006. Review of three-dimensional ecological modelling related to the North Sea shelf system. Part II: Model validation and data needs. Oceanography & Marine Biology - Annual Review 44: 1-60.

Raine, R., Joyce, B., Richard, J., Pazos, Y., Moloney, M., Jones, K., Patching, J.W., 1993. The development of an exceptional bloom of the dinoflagellate *Gyrodinium aureolum* on the southwest Irish coast. ICES Journal of Marine Science 50: 461-469.

Raine, R., McDermott, G., Silke, J., Lyons, K., Cusack, C., 2010. A simple short range model for the prediction of harmful algal events in the bays of southwestern Ireland. Journal of Marine Systems 83: 150-157.

Recknagel, F., 1997. ANNA - Artificial Neural Network model for predicting species abundance and succession of blue-green algae. Hydrobiologia 349: 47-57.

Reid, P.C., Lancelot, C, Gieskes, W.W.C, Hagmeier, E., Weichart, G., 1990. Phytoplankton of the North Sea and its dynamics: a review. Journal of Sea Research 26: 295-331.

Reynolds, C.S., Wiseman, S.W., Godfrey, B.M., Butterwick, C., 1983. Some effects of artificial mixing on the dynamics of phytoplankton populations in large limnetic enclosures. Journal of Plankton Research 5: 203-234.

Richardson, A.J., Schoeman, D.S., 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. Science 305: 1609-1612.

Riebesell, U., 1991. Particle aggregation during a diatom bloom. I. Physical aspects. Marine Ecology Progress Series 69: 273-280.

Riegman, R, Noordeloos, A.A.M., Cadee, G.C., 1992, *Phaeocystis* blooms and eutrophication of the continental coastsal zones of the North Sea, Marine Biology 112: 479-484.

Riemann, B., Simonsen, P., Stensgaard, L., 1989. The carbon and chlorophyll content of phytoplankton from various nutrient regimes. Journal of Plankton Research 11: 1037-1045.

Rinta-Kanto, J.M., Ouellette, A.J.A., Boyer, G.L., Twiss, M.R., Bridgeman, T.B., et al., 2005. Quantification of toxic *Microcystis* spp. during the 2003 and 2004 blooms in western Lake Erie using quantitative real-time PCR. Environmental Science Technology 39: 4198-4205.

Roiha, P., Westerlund, A., Nummelin, A., Stipa, T., 2010. Ensemble forecasting of harmful algal blooms in the Baltic Sea. Journal of Marine Systems 83: 210-220.

Roncarati, F., Rijstenbil, J.W., Pistocchi, R., 2008. Photosynthetic performance, oxidative damage and antioxidants in *Cylindrotheca closterium* in response to high irradiance, UVB radiation and salinity. Marine Biology153: 965-973.

Rousseau, V., Chrétiennot-Dinet, M-J., Jacobsen, A., Verity, P., Whipple, S., 2007. The life cycle of *Phaeocystis*: state of knowledge and presumptive role in ecology. Biogeochemistry 83: 29-47.

Rousseau, V., Leynaert, A., Daoud, N., Lancelot, C., 2002. Diatom succession, silicification and silicic acid availability in Belgian coastal waters (Southern North Sea). Marine Ecology Progress Series 236: 61-73.

Rousseau, V., Mathot, S., Lancelot, C., 1990. Conversion factors for the determination of *Phaeocystis* sp. Carbon biomass in the Southern Bight of the North Sea on the basis of microscopical observations. Marine Biology 107: 305-314.

Ruddick, K.G., Gons, H.J., Rijkeboer, M., Tilstone, G., 2001. Optical remote sensing of chlorophyll a in case 2 waters by use of an adaptive two-band algorithm with optimal error properties. Applied Optics 40: 3575-3585.

Ruokanen, L., Kaitala, S., Fleming, V., Maunula, P., 2003. Alg@line: joint operational unattended phytoplankton monitoring in the Baltic Sea. Elsevier Oceanography Series 69: 519-522.

Rutten, T.P.A., Sandee, B., Hofman, A.R.T., 2005. Phytoplankton monitoring by high performance flow cytometry: A successful approach? Cytometry 64A: 16-26.

Salacinska, K., 2008. Sensitivity analysis of the 2D application of the Generic Ecological Model to the North Sea. MSc thesis, Delft University of Technology, Delft, The Netherlands, 84 pp.

Saltelli, A., Tarantola, S., Campolongo, F., Ratto, M., 2004. Sensitivity analysis in practice: a guide to assessing scientific models. Halsted Press, New York, NY, 2004.

Schiller, H., Doerffer, R. 2005. Improved Determination of Coastal Water Constituent Concentrations From MERIS Data. IEEE Transactions on Geoscience and Remote Sensing 43: 1585-1591.

Schoemann, V., Becquevort, S., Stefels, J., Rousseau, V., Lancelot, C., 2005. *Phaeocystis* blooms in the global ocean and their controlling mechanisms: a review. Journal of Sea Research 53: 43-66.

Schofield, O. Grzymski, J., Bissett, W.P., Kirkpatrick, G.J., Millie, D.F., Moline, M., Roesler, C., 1999. Optical monitoring and forecasting systems for harmful algal blooms: possibility or pipe dream? Journal of Phycology 35: 1477-1496.

Scholten, H., Van der Tol, W.M., 1994. SMOES: a simulation model for the Oosterschelde ecosystem Part 2: Calibration and validation. Hydrobiologia 282/283: 453-474.

Seuront, L. Vincent, D., Mitchell, J.G., 2006. Biologically induced modification of seawater viscosity in the Eastern English Channel during a *Phaeocystis globosa* spring bloom. Journal of Marine Systems 61: 118-133.

Sfriso, A., Facca, C., Ghetti, P.F., 2003. Temporal and spatial changes of macroalgae and phytoplanton in a Mediterranean coastal area: the Venice Lagoon as a case study. Marine Environmental Research 56: 617-636.

Sharples, J., 2008. Potential impacts of the spring-neap tidal cycle on shelf sea primary production. Journal of Plankton Reserach 30: 183-197.

Sharples, J., Ross, O.N., Scott, B.E., Greenstreet, S.P., Fraser, H., 2006. Inter-annual variability in the timing of stratification and the spring bloom in the North-western North Sea. Continental Shelf Research 26: 733-751.

Sharples, J., Tweddle, J.F., Green, J.A.M., Palmer, M.R., Kim, Y.N., et al., 2007. Spring-neap modulation of internal tide mixing and vertical nitrate fluxes at a shelf edge in summer. Limnology and Oceanography 52: 1735-1747.

Shifrin, N.S., Chisholm, S.W., 1981. Phytoplankton lipids: interspecific differences and effects of nitrate, silicate and light-dark cycles. Journal of Phycology 17: 374-384.

Simis, S.G., Peters, S.W., Gons, H.J., 2005. Remote sensing of the cyanobacterial pigment phycocyanin in turbid inland water. Limnology and Oceanography 50: 237-245.

Simis, S.G., Ruiz-Verdú, A., Domínguez-Gómez, J.A., Peña-Martinez, R., Peters, S.W., Gons, H.J., 2007. Influence of phytoplankton pigment composition on remote sensing of cyanobacterial biomass. Remote Sensing of Environment 106: 414-427.

Simpson, J.H., Bos, W.G., Schirmer, F., Souza, A.J., Rippeth, T.P., et al.,1993. Periodic stratification in the Rhine ROFI in the North Sea. Oceanologica Acta 16: 23-32.

Skogen, M.D., Svendsen, E., Aksnes, D., Ulvestad, K.B., 1995. Modeling the primary production in the North Sea using a coupled 3-dimensional physical-chemical-biological ocean model. Estuarine, Coastal and Shelf Science 21: 545-565.

Smayda, T., 1971. Normal and accelerated sinking of phytoplankton in the sea. Marine Geology 11: 105-122.

Smayda, T.J. 1998. Patterns of variability characterizing marine phytoplankton, with examples from Narragansett Bay. ICES Journal of Marine Science 55: 562-573.

Smetacek, V.S., 1985. Role of sinking in diatom life-history cycles:ecological, evolutionary and geological significance. Marine Biology 84: 239-251.

Smits, J., 2006. Environmental Master Plan and Investment Strategy for the Marmara Sea Basin. Water Quality Modelling of the Sea of Marmara: Model development and scenario simulations. WL | Delft Hydraulics, technical report Z3804.50, October 2006, 167 pp.

Smythe-Wright, D., Daniel, A., Boswell, S., Purcell, D., Hartman, M., et al., 2014. Phytoplankton and pigment studies in the Bay of Biscay and English Channel. Deep Sea Research Part II: Topical Studies in Oceanography (in press).

Soetaert, K., Herman, P.M.J., 1995a. Carbon flows in the Westerschelde estuary (the Netherlands) evaluated by means of an ecosystem model (MOSES). Hydrobiologia 311: 247-266.

Soetaert, K., Herman, P.M.J., 1995b. Nitrogen dynamics in the Westerschelde estuary (SW Netherlands) estimated by means of the ecosystem model MOSES. Hydrobiologia 311: 225-246.

Soetaert, K., Herman, P.M.J., Kromkamp, J., 1994. Living in the twilight: estimating net phytoplankton growth in the Westerschelde estuary (The Netherlands) by means of an ecosystem model (MOSES). Journal of Plankton Research 16: 1277-1301.

Sommer, U., 1985. Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. Limnology and Oceanography 30: 335-346.

Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J.J., Gaedke, U., et al., 2012. Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. Annual Review of Ecology, Evolution, and Systematics 43: 429-448.

Sosik, H.M., Olson, R.J., 2007. Automated taxonomic classification of phytoplankton sampled with imaging-in-flow cytometry. Limnology and Oceanography Methods 5: 204-216.

Stenseth N.C., Llope M., Anadón R., Ciannelli L., Chan K., Hjermann D.Ø., Bagøien E., Ottersen G., 2006. Seasonal plankton dynamics along a cross-shelf gradient. Proceedings of the Royal Society London B 273: 2831-2838.

Stock, C.A., McGillicuddy Jr, D.J., Anderson, D.M., Solow, A.R., Signell, R.P., 2007. Blooms of the toxic dinoflagellate *Alexandrium fundyense* in the western Gulf of Maine in 1993 and 1994: a comparative modeling study. Continental Shelf Research 27: 2486-2512.

Stock, C.A., McGillicuddy Jr, D.J., Solow, A.R., Anderson, D.M., 2005. Evaluating hypotheses for the initiation and development of *Alexandrium fundyense* blooms in the western Gulf of Maine using a coupled physical–biological model. Deep Sea Research Part II: Topical Studies in Oceanography 52: 2715-2744.

Stomp, M., Huisman, J., Stal, L.J., Matthijs, H.C.P., 2007. Colorful niches of phototrophic microorganisms shaped by vibrations of the water molecule. ISME Journal 1: 271-282.

Stomp, M., van Dijk, M.A., van Overzee, H.M.J., Wortel, M., Sigon, C., et al., 2008. The timescale of phenotypic plasticity and its impact on competition in fluctuating environments. American Naturalist 172: E169-E185.

Stumpf, R.P, Tomlinson, M.C., 2005. Remote Sensing of Harmful Algal Blooms, in Remote Sensing of Coastal Aquatic Environments, R.L. Miller, C.E. del Castillo and B.A. McKee (eds), Springer, Dordrecht, The Netherlands, ISBN 1-4020-3099-1, 277-296.

Stumpf, R.P., Culver, M.E., Tester, P.A., Tomlinson, M., Kirkpatrick, G.J., et al., 2003. Monitoring *Karenia brevis* blooms in the Gulf of Mexico using satellite ocean color imagery and other data. Harmful Algae 2: 147-160.

Stumpf, R.P., Tomlinson, M.C., Calkins, J.A., Kirkpatrick, B., Fisher, K., et al., 2009. Skill assessment for an operational algal bloom forecast system. Journal of Marine Systems 76: 151-161.

Sutherland, T.F., Grant, J., Amos, C.L., 1998. The effect of carbohydrate production by the diatom *Nitzschia curvilineata* on the erodibility of sediment. Limnology and Oceanography 43: 65-72.

Sverdrup, H.U., 1953. On conditions for the vernal blooming of phytoplankton. ICES Journal of Marine Science: Journal du Conseil 18: 287-295.

Tang, D.L., Kawamura, H., Doan-Nhu, H., Takahashi, W., 2004. Remote sensing of a harmful algal bloom off the coast of southeastern Vietnam. Journal of Geophysical Research 109: C03014.

Tett, P.B., 1987. Plankton. In: Baker JM, Wolff JW, editors. Biological surveys of estuaries and coasts. Cambridge University Press. pp. 280-341.

Thornton, D.C.O., 2002. Diatom aggregation in the sea: mechanisms and ecological implications. European Journal of Phycology 37: 149-161.

Thurstan, R.H., Brockington, S., Roberts, C.M., 2010. The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nature Communications 1: 15.

Thyssen, M., Garcia, N., Denis, M., 2009. Sub meso scale phytoplankton distribution in the North East Atlantic surface waters determined with an automated flow cytometer. Biogeosciences 6: 569-583.

Thyssen, M., Mathieu, D., Garcia, N., Denis, M., 2008. Short-term variation of phytoplankton assemblages in Mediterranean coastal waters recorded with an automated submerged flow cytometer. Journal of Plankton Research 30: 1027-1040.

Tian, T., Merico, A., Su, J., Staneva, J., Wiltshire, K., et al., 2009. Importance of resuspended sediment dynamics for the phytoplankton spring bloom in a coastal marine ecosystem. Journal of Sea Research 62: 214-228.

Tilman, D., 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58: 338-348.

Tilstone, G., van der Woerd, H., Krasemann, H., Martinez-Vicente, V., Blondeau- Patissier, D., Eleveld., M., Høkedal, J., Jorgensen, P., Pasterkamp, Peters, S.R., Röttgers, R., Schoenfeld,W., Sørensen, K., 2010. Variation in absorption properties of European coastal waters: application to ocean colour satellite algorithms. Journal of Geophysical Research Submitted.

Tilstone, G.H., Peters, S.W., van der Woerd, H.J., Eleveld, M.A., Ruddick, K., et al., 2012. Variability in specific-absorption properties and their use in a semi-analytical ocean colour algorithm for MERIS in North Sea and Western English Channel coastal waters. Remote Sensing of the Environment 118: 320-338.

Torrence, C., Compo, G.P., 1998. A practical guide to wavelet analysis. Bulletin of the American Meteorological Society 79: 61-78.

UNEP, 2006. Marine and coastal ecosystems and human well-being: A synthesis report based on the findings of the Millennium Ecosystem Assessment. UNEP, 76 pp.

Utermöhl, H., 1931. Neue Wege in der quantitativen Erfassung des Planktons. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 5: 567-595.

van Boekel, W.H.M., Hansen, F.C., Riegman, R., Bak, R.P.M., 1992. Lysis-induced decline of a *Phaeocystis* spring bloom and coupling with the microbial foodweb. Marine Ecology Progress Series 81: 269-276.

Van Bracht, M.J., 2001. Made to measure: information requirements and groundwater level monitoring networks. PhD thesis, Free University of Amsterdam, The Netherlands.

Van de Wolfshaar, K.E., 2007. Beoordeling Generiek Ecologisch Model, GEM. Report summarising the outcome of an international audit of the GEM model. WL | Delft Hydraulics, technical report Z4267, January 2007, 47 pp.

Van der Fels-Klerx, H.J., Adamse, P., Goedhart, P.W., Poelman, M., Pol-Hofstad, I.E., et al., 2012. Monitoring phytoplankton and marine biotoxins in production waters of the Netherlands: results after one decade. Food Additives & Contaminants: Part A, 29: 1616-1629.

Van der Molen, D.T., Los, F.J., Van der Tol, M., 1994. Mathematical modelling as a tool for management in eutrophication control of shallow lakes. Hydrobiologia 275/276: 479-492.

Van der Woerd, H.J., Blauw, A., Pasterkamp, R., Tatman, S., Laanen, M., Peperzak, L., 2005. Integrated spatial and spectral characterisation of harmful algal blooms in Dutch coastal waters (ISCHA)-Demonstration of a HAB service in the Zeeuwse Voordelta. IVM report R 05/09, Amsterdam, The Netherlands.

Van der Woerd, H.J., Blauw, A., Peperzak, L., Pasterkamp, R., Peters, S., 2011. Analysis of the spatial evolution of the 2003 algal bloom in the Voordelta (North Sea). Journal of Sea Research 65: 195-204.

Van Der Woerd, H.J., Pasterkamp, R., 2008. HYDROPT: a fast and flexible method to retrieve chlorophyll-a from multispectral satellite observations of optically complex coastal waters. Remote Sensing of the Environment 112: 1795-1807.

Van Gils, J., 1998. The SOBEK Processes Editor: a flexible tool for tailor-made water quality modelling. In Babovic, V. & L.C. Larsen (eds), Proceedings of the Third International Conference on Hydroinformatics, Copenhagen, Denmark. Balkema, Rotterdam: 591-595.

Van Gils, J.A.G., Ouboter, M.R.L., De Rooij, N.M., 1993. Modelling of water sediment quality in the Scheldt Estuary. Netherlands Journal of Aquatic Ecology 27: 257-265.

Van Haren, H., Mills, D.K., Wetsteyn, L.P.M.J., 1998. Detailed observations of the phytoplankton spring bloom in the stratifying central North Sea. Journal of Marine Research 56: 655-680.

Van Leussen, W., 2011. Macroflocs, fine-grained sediment transports, and their longitudinal variations in the Ems Estuary. Ocean Dynamics 61: 387-401.

Van Leussen, W., Radach, G., van Raaphorst, W., Colijn, F., Laane R.,1996. The North-West European Shelf Programme (NOWESP): integrated analysis of shelf processes based on existing data sets and models ICES Journal of Marine Science 53: 926-932.

van Raaphorst, W., Kloosterhuis, H.T., 1994. Phosphate sorption in superficial intertidal sediments. Marine Chemistry 48: 1-16.

Veldhuis, M. J. W., Brussaard, C., Noordeloos, A., 2005. Living in a *Phaeocystis* colony; a way of accerelating growth. Harmful Algae 4: 841-858.

Veldhuis, M.J.W., Admiraal, W., Colijn, F., 1986. Chemical and physiological changes of phytoplankton during the spring bloom, dominated by *Phaeocystis pouchetii* (Haptophyceae): observations in Dutch coastal waters of the North Sea. Netherlands Journal of Sea Research 20: 49-60.

Veldhuis, M.J.W., Colijn, F., Admiraal, W., 1991. Phosphate utilization in *Phaeocystis pouchetii* (Haptophyceae). Marine Ecology 12: 53-62.

Velo-Suárez, L., Gutiérrez-Estrada, J.C., 2007. Artificial neural network approaches to one-step weekly prediction of *Dinophysis acuminata* blooms in Huelva (Western Andalucía, Spain). Harmful Algae 6: 361-371.

Volterra, V., 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118: 558-560.

Weijerman, M., Lindeboom, H., & Zuur, A.F., 2005. Regime shifts in marine ecosystems of the North Sea and Wadden Sea. Marine Ecology Progress Series 298: 21-39.

Weston, K., Fernand, L., Mills, D.K., Delahunty, R., Brown, J., 2005. Primary production in the deep chlorophyll maximum of the central North Sea. Journal of Plankton Research 27: 909-922.

Weston, K., Greenwood, N., Fernand, .L, Pearce, D.J., Sivyer, D.B., 2008. Environmental controls on phytoplankton community composition in the Thames plume, U.K. Journal of Sea Research 60: 246-254.

Whipple, S.J., Patten, B.C., Verity, P.G., 2005. Life cycle of the marine alga *Phaeocystis*: a conceptual model to summarize literature and guide research. Journal of Marine Systems 57: 83-110.

Widdicombe, C.E., Eloire, D., Harbour, D., Harris, R.P., Somerfield, P.J., 2010. Long-term phytoplankton community dynamics in the Western English Channel. Journal of Plankton Research 32: 643-655.

Wiltshire, K.H., Kraberg A., Bartsch, I., Boersma, M., Franke, H.D., et al., 2010. Helgoland roads, North Sea: 45 years of change. Estuaries and Coasts 33: 295-310.

Winder, M., Cloern, J.E., 2010. Annual cycles of phytoplankton biomass. Philosophical Transactions of the Royal Society B-Biological Sciences 365: 3215-3226.

WL | Delft Hydraulics, 2002. GEM documentation and user manual. WL | Delft Hydraulics, technical document Z3197, Delft, The Netherlands.

WL | Delft Hydraulics, 2003. Delft3D-WAQ users manual. WL | Delft Hydraulics, Delft, The Netherlands.

Wood, S., 2006. Generalized additive models: an introduction with R. CRC press.

Wood, S.N., 2013. On p-values for smooth components of an extended generalized additive model. Biometrika 100: 221-228.

Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F., Hairston, N.G. Jr., 2003. Rapid evolution drives ecological dynamics in a predator-prey system. Nature 424: 303-306.

Zadeh, L., 1965. Fuzzy sets. Information and Controls 8: 338-353.

# Summary

The North Sea is a coastal shelf sea receiving water from many large rivers. Therefore the North Sea is rich in nutrients and phytoplankton. Phytoplankton forms the base of the marine food web and produces approximately 50% of total global primary production. Through the uptake of carbon dioxide for growth phytoplankton strongly affects the global climate. However, too high concentrations phytoplankton can also have negative impacts on ecosystems, such as oxygen depletion and shellfish mortality. To reduce negative impacts of algal blooms, countries bordering the North Sea agreed to reduce nutrient inputs from rivers with 50% compared to peak levels in 1985. They also agreed to regularly monitor concentrations of nutrients, phytoplankton and oxygen to check if eutrophication problems were reduced. Since then, measurements show a strong reduction of phosphate concentrations and a modest reduction of nitrate concentrations. A significant decrease of phytoplankton concentrations has not been observed. The absence of a significant trend may imply that nutrient reduction has not affected phytoplankton concentrations. Alternatively, phytoplankton concentrations may have decreased but this was not detected because the natural variability of phytoplankton concentrations masked this trend or because the monitoring frequency was too low to detect a significant trend.

During recent years, monitoring vessels of Rijkswaterstaat have collected water samples at fixed locations at sea to measure concentrations of phytoplankton and other variables. The monitoring frequency and the number of monitoring stations have been reduced in several phases to reduce costs. Yet, phytoplankton concentrations are strongly variable in space and time. Therefore, a high monitoring frequency at many locations is required to capture the natural variability of phytoplankton and detect trends. Novel automated monitoring methods are being developed that can acquire information on phytoplankton abundance at a high resolution in space and time, such as satellite remote sensing, moorings and automated measurements from ferries. The resulting high-resolution data sets enable characterization of phytoplankton variability at different time scales and identification of the mechanisms driving phytoplankton variability.

In this thesis phytoplankton variability in the North Sea is investigated with a range of traditional and novel monitoring methods. We characterized the variability in space and time and analysed the drivers of this variability at different time scales with various methods for data analysis and modeling. In this way we gained experience with the analysis and interpretation of data from automated monitoring methods. Our results demonstrate the potential power of these novel techniques, providing a much improved understanding of population fluctuations at several different time scales. Based on this

understanding appropriate monitoring strategies can be designed to assess the response of phytoplankton to changes in nutrient inputs and global climate change.

Phytoplankton requires nutrients and light to maintain growth. Based on the availability of nutrients and light and current patterns we could reproduce observed spatial and seasonal patterns of phytoplankton in the southern North Sea with the Generic Ecological Model (GEM). Algal blooms of the species *Phaeocystis* can cause large economic losses for mussel farmers in the Eastern Scheldt and foam accumulation on beaches. We tested the feasibility of an early-warning system for *Phaeocystis* blooms in the Eastern Scheldt area combining satellite remote sensing, field measurements and the GEM model. For this purpose, we checked to what extent information on total phytoplankton and *Phaeocystis* in spring 2003 agreed between these different data sources. The bloom period of total phytoplankton was similar in the different data sources. Available field data for *Phaeocystis* had too low temporal and spatial resolution to assess if model results for *Phaeocystis* and satellite data of chlorophyll were a good approximation of actual *Phaeocystis* concentrations.

As alternative approach to predict nuisance *Phaeocystis* bloom events we developed a fuzzy logic model. Fuzzy logic models use knowledge rules based on patterns in observed data and understanding of relevant processes. With this model the initiation of *Phaeocystis* blooms in Dutch coastal waters could be reproduced. Differences in long-term averaged *Phaeocystis* concentrations between stations were strongly associated with differences in local nutrient concentrations. Interannual variation in *Phaeocystis* concentrations could not be reliably assessed with the available data series, due to the low sampling frequency of once or twice per month. Video images of the beach with ARGUS camera's from a light house provided information on foam presence on the beach with an hourly resolution. These data showed a strong dependence of foam accumulation on wind conditions: foam was only visible during moderate to strong landward winds. Within the European research project HABES (Harmful Algal Blooms Expert Systems) similar fuzzy logic models have been developed for the 5 dominant harmful algal species in 5 marine areas throughout Europe. This showed that fuzzy logic models offer a good approach to synthesize all available knowledge about specific harmful algal blooms and use it for predictions. The approach enables to include all known aspects of bloom formation, even if not all underlying processes are understood in detail.

In the previous analyses the temporal resolution of observed data was often limiting a good assessment of phytoplankton variability. Automated moorings can provide data series with high temporal resolution. We analysed the data of four mooring stations in the North Sea to assess the extent and the drivers of phytoplankton variability. In coastal waters near the Thames estuary the tidal cycle was the dominant driver of short-term phytoplankton variability. Phytoplankton fluctuations showed strong 6-hour periodicity in phase with fluctuations in tidal current speeds, 12-hour periodicity in phase with ebb and flood and 15-day periodicity in phase with the spring-neap tidal cycle. This suggests that phytoplankton not only moves back and forth with the tide (with a 12-hour periodicity) but also sinks during decreasing tidal currents and mixes back to the surface at increasing tidal currents (with a 6-hour and 15-day periodicity); as if they dance with the tide. In deeper waters in the central North Sea, the tide had little impact on phytoplankton. Phytoplankton fluctuations in this area were predominantly controlled by vertical mixing and sinking induced by fluctuations in wind and solar irradiance. In Dutch coastal waters phytoplankton fluctuations were strongly associated with fluctuations in salinity due to the influence of fresh water from the river Rhine. At all four moorings sinking and mixing of phytoplankton particles appeared to be a dominant driver of fluctuations in phytoplankton concentrations.

The analyses in this thesis have shown that data series of high temporal resolution are required to detect changes in phytoplankton concentrations and underlying mechanisms. For accurate assessment of interannual variability in phytoplankton concentrations a sampling frequency of once or twice per week seems to be sufficient. To detect relations between phytoplankton change and environmental conditions an hourly to daily sampling frequency is required. Novel automated monitoring methods such as satellite remote sensing, moorings and sensors on board of ferries enable data acquisition at such high resolution.

# Samenvatting

De Noordzee is een relatief ondiepe zee, waarin veel grote rivieren uitmonden. Hierdoor is de Noordzee rijk aan nutriënten en fytoplankton. Fytoplankton vormt de basis voor het mariene voedselweb, is verantwoordelijk voor ca. 50% van de totale primaire productie op aarde, en heeft door de vastlegging van CO2 een belangrijke invloed op het klimaat. Te hoge concentraties fytoplankton kunnen echter negatieve effecten hebben op het milieu, zoals zuurstofloosheid van het water en sterfte van schelpdierpopulaties. Om negatieve effecten door dergelijke algenbloeien te beperken is door de landen rond de Noordzee afgesproken om de aanvoer van nutriënten door rivieren naar de Noordzee te halveren ten opzichte van 1985, toen de aanvoer op zijn hoogst was. Ook is afgesproken om de concentraties van nutriënten, fytoplankton en zuurstof regelmatig te meten om te controleren of de problemen door overmatige algengroei (eutrofiëring) afnemen. Sindsdien laten metingen een sterke afname zien van het nutriënt fosfaat en een bescheiden afname van het nutriënt nitraat. Significante trends in fytoplanktonconcentraties als gevolg van deze afname in nutriëntenconcentraties zijn nog niet waargenomen. Dit kan verschillende oorzaken hebben. Het kan zijn dat fytoplanktonconcentraties niet zijn afgenomen, of dat de natuurlijke variatie in algenconcentraties zo groot is dat de trend daardoor niet kan worden vastgesteld, of dat de meetfrequentie te laag was om effecten vast te stellen.

Voor het meten van concentraties fytoplankton en andere variabelen hebben schepen van Rijkswaterstaat de afgelopen tientallen jaren watermonsters genomen op een netwerk van vaste meetlokaties op zee. Om kosten te besparen is de frequentie van de metingen en het aantal meetlokaties in een aantal stappen verlaagd. Fytoplanktonconcentraties variëren sterk in tijd en ruimte, waardoor eigenlijk een hoge meetfrequentie nodig is op een groot aantal lokaties om een goed beeld te krijgen van de fytoplanktondynamiek en om eventuele veranderingen hierin te detecteren. Nieuwe geautomatiseerde meetmethoden zijn in ontwikkeling om informatie over fytoplanktonconcentraties te verkrijgen met een grotere resolutie in ruimte en tijd, zoals satellietbeelden, meetboeien en automatische metingen vanaf veerboten. Hierdoor komen nu meetgegevens beschikbaar waarmee de mate van variabiliteit in fytoplankton zichtbaar wordt en waarmee de oorzaken van deze variabiliteit kunnen worden onderzocht.

In dit proefschrift is onderzocht in hoeverre de variabiliteit van fytoplankton in de Noordzee kan worden verklaard door variabiliteit in milieuomstandigheden. Hierbij is gebruik gemaakt van gegevens van traditionele en nieuwe geautomatiseerde meet-methoden en van diverse methoden voor analyse en modellering. Op basis hiervan kan

worden ingeschat wat de mogelijke gevolgen zijn van veranderingen in nutriëntenaanvoer of klimaat en hoe deze het beste kunnen worden gemeten.

Fytoplankton heeft nutriënten en licht nodig om te kunnen groeien. Op basis van de beschikbaarheid van nutriënten en licht en stromingspatronen konden we met het Generiek Ecologisch Model (GEM) de ruimtelijke patronen en seizoensdynamiek van fytoplankton in de zuidelijke Noordzee goed reproduceren. Algenbloeien van de soort *Phaeocystis globosa* kunnen grote schade veroorzaken voor mosselkwekers in de Oosterschelde en leiden vaak tot schuimophoping op het strand. We hebben een waarschuwingssysteem ontwikkeld voor *Phaeocystis* bloeien in de Oosterschelde op basis van satellietmetingen, veldmetingen en het GEM model. Hiervoor hebben we gekeken in hoeverre de informatie uit deze verschillende informatiebronnen overeen kwam voor totaal fytoplankton en *Phaeocystis* in het voorjaar van 2003. De bloeiperiode van totaal fytoplankton was vergelijkbaar in de verschillende datasets. De beschikbare veldmetingen van *Phaeocystis* hadden een te lage ruimtelijke en temporele resolutie om te zien of de modelresultaten voor *Phaeocystis* of de satellietmetingen van chlorofyl goed overeen kwamen met de werkelijke *Phaeocystis* concentraties.

Als alternatieve benadering om *Phaeocystis* bloeien te voorspellen hebben we een fuzzy logic model gemaakt. In fuzzy logic wordt gebruik gemaakt van kennisregels op basis van patronen in beschikbare meetgegeven en globale kennis over relevante processen. Het model kon de start van het bloeiseizoen van *Phaeocystis* in Nederlandse kustwateren goed reproduceren. Verschillen tussen stations in het langjarig gemiddelde van de *Phaeocystis* concentraties vertoonden een sterk verband met lokale nutriëntenconcentraties. Verschillen in *Phaeocystis* concentraties tussen jaren konden met de beschikbare meetgegevens niet goed worden gekwantificeerd, door de lage meetfrequentie van 1 tot 2 keer per maand. Videobeelden van het strand met ARGUS camera's leverden uurlijkse informatie over het voorkomen van schuim op het strand bij Noordwijk. Hierdoor kon een sterke relatie met windomstandigheden worden aangetoond: schuim kwam alleen voor bij sterke aanlandige wind. Binnen het Europese onderzoeksproject HABES zijn soortgelijke fuzzy logic modellen ontwikkeld voor de belangrijkste schadelijke algensoorten in Europa. Hieruit bleek dat fuzzy logic modellering een goede manier is om alle beschikbare informatie over bloeien van een algensoort te bundelen en toetsbaar te maken. Hierdoor kunnen de meest relevante aspecten worden meegenomen in de analyse van algenbloeien, voordat alle onderliggende processen tot in detail bekend zijn.

In de voorgaande analyses was de temporele resolutie van meetgegevens vaak een beperkende factor om de variabiliteit in fytoplankton concentraties goed in beeld te krijgen. Met geautomatiseerde meetboeien kunnen meetreeksen met hoge temporele resolutie worden verkregen. We hebben de meetgegevens van vier meetboeien in de

Noordzee geanalyseerd om te achterhalen welke processen verantwoordelijk zijn voor fluctuaties in fytoplankton concentraties. In zuid-Engelse kustwateren bleek het getij de belangrijkste oorzaak: fytoplankton concentraties vertoonden sterke 6-uurlijkse fluctuaties in fase met fluctuaties in de stroomsnelheden van het opkomend en neergaand getij, 12-uurlijkse fluctuaties in fase met eb en vloed, en 15-daagse fluctuaties in fase met de springtij doodtij cyclus. Dit suggereert dat deze microscopisch kleine algen niet alleen heen en weer stromen met het getij (met een 12-uurlijkse cyclus), maar ook zinken tijdens afnemende getijstroming en opwervelen bij toenemende getijstroming (met een 6-uurlijkse en 15-daagse cyclus). Ze dansen als het ware op het ritme van het getij op en neer. In de diepe wateren van de centrale Noordzee was de invloed van het getij gering en waren korte termijn fluctuaties in algenconcentraties voornamelijk gekoppeld aan vertikale menging onder invloed van wind and zoninstraling. Langs de Nederlandse Noordzee kust waren korte termijn fluctuaties in algenconcentraties voornamelijk gerelateerd aan fluctuaties in zoutgehalte veroorzaakt door de menging met zoet rivierwater van de Rijn. Op alle stations bleek het zinken en opwervelen van algen een belangrijke oorzaak van de fluctuaties in fytoplankton concentraties.

De analyses in dit proefschrift hebben duidelijk gemaakt dat meetreeksen met hoge temporele resolutie noodzakelijk zijn om veranderingen in fytoplankton concentraties en de onderliggende oorzaken in beeld te brengen. Voor het betrouwbaar schatten van verschillen in algenconcentraties tussen jaren lijkt een wekelijkse frequentie toereikend. Om relaties met omgevingsfactoren zichtbaar te maken is een uurlijkse tot dagelijkse meetfrequentie nodig. Dergelijke hoge meetfrequenties worden mogelijk gemaakt door automatische meetmethoden, zoals meetboeien, sensoren aan boord van veerboten en satellietbeelden.

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# Curriculum Vitae

Anouk Blauw was born in Rotterdam on 26 April 1972. After finishing high school at the Coornhert Gymnasium in Gouda she studied environmental science in Wageningen from 1990 to 1996. During her studies she specialized in ecological water management. After her studies she worked at the consulting company Witteveen and Bos on mostly urban water management. In 1998 she joined Deltares (formerly called WL | Delft Hydraulics) where she worked on ecological modelling of coastal waters, with a focus on phytoplankton. Both as project leader and team member she has participated in national and international projects on marine phytoplankton. These included studies aiming at reduction of eutrophication in the North Sea, the Philippines and the Sea of Marmara using Delft3D modelling. Also she used Delft3D to estimate carrying capacity for shellfish aquaculture in Dutch, Irish and Scottish waters. From 2000 to 2003 Anouk Blauw led the European research project HABES (Harmful Algal Blooms Expert System). In this project fuzzy logic models were developed predicting harmful algal blooms of the 5 dominant harmful algal species in five marine areas across Europe. Subsequently she contributed to the development of a harmful algal bloom information service for the Eastern Scheldt in the Netherlands combining operational Delft3D modelling, with near real time satellite remote sensing and field measurements. In 2009 she started a PhD-project on "Integrated monitoring of the carrying capacity of coastal waters" at the University of Amsterdam, which resulted in this PhD-thesis. At present Anouk works as senior scientist at Deltares again on monitoring strategies and prediction of phytoplankton dynamics, including harmful algal blooms.

## PUBLICATIONS:


- Blauw, A.N., Benincà, E., Laane, R.W.P.M., Greenwood, N., Huisman, J., 2012. Dancing with the tides: fluctuations of coastal phytoplankton orchestrated by different oscillatory modes of the tidal cycle. PLoS ONE 7(11): e49319.
- Van der Woerd, H.J., Blauw, A., Peperzak, L., Pasterkamp, R., Peters, S., 2011. Analysis of the spatial evolution of the 2003 algal bloom in the Voordelta (North Sea). Journal of Sea Research 65: 195-204.
- Blauw, A.N., Los, F.J., Huisman, J., Peperzak, L., 2010. Nuisance foam events and *Phaeocystis globosa* blooms in Dutch coastal waters analyzed with fuzzy logic. Journal of Marine Systems 83: 115-126.
- Li, H., Arias, M., Blauw, A., Los, H., Mynett, A.E., Peters, S., 2010. Enhancing generic ecological model for short-term prediction of Southern North Sea algal dynamics with remote sensing images. Ecological Modelling 221: 2435-2446.
- Salacinska, K., El Serafy, G.Y., Los, F.J., Blauw, A., 2010. Sensitivity analysis of the two dimensional application of the Generic Ecological Model (GEM) to algal bloom prediction in the North Sea. Ecological Modelling 221:178-190.
- Blauw, A.N., Los, H.F.J., Bokhorst, M., Erftemeijer, P.L.A., 2009. GEM: a generic ecological model for estuaries and coastal waters. Hydrobiologia 618: 175-198.
- Blauw, A.N., Anderson, P., Estrada, M., Johansen, M., Laanemets, J., et al., 2006. The use of fuzzy logic for data analysis and modelling of European harmful algal blooms: results of the HABES project. African Journal of Marine Science 28: 365-369.
- Widdows, J., Blauw, A., Heip, C.H.R., Herman, P.M.J., Lucas, C.H., Middelburg, J.J., Schmidt, S., Brinsley, M.D., Twisk, F., Verbeek, H., 2004. Role of physical and biological processes in sediment dynamics of a tidal flat in Westerschelde Estuary, SW Netherlands. Marine Ecology Progress Series 274: 41-56.