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**A sea of change**

*Impacts of reduced nitrogen and phosphorus loads on coastal phytoplankton communities*

Burson, A.M.

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## Summary

### A Sea of Change:

#### *Impacts of Reduced Nitrogen and Phosphorus Loads on Coastal Phytoplankton Communities*

The amount of nutrients entering the North Sea and many other coastal waters is highly impacted by anthropogenic activities. For decades, nutrient loading has steadily increased, which eventually resulted in eutrophication of coastal marine ecosystems. To address the negative impacts of nutrient loading, a multi-national agreement was enacted in 1986, to reduce by half the total nitrogen and phosphorus loads entering the North Sea via the major rivers of western Europe. By the early 2000s, the reduction of total phosphorus, at 50-70%, was more successful than the reduction of total nitrogen, at 20-30%. This disproportionate reduction in major nutrients may affect the productivity, species composition and nutritional quality of marine phytoplankton, at the base of the marine food web. To understand how this shift in nutrient loads has impacted the phytoplankton community in the North Sea, three major aims were addressed in this thesis.

- The first aim is to determine if multi-decadal de-eutrophication efforts have changed the nutrient stoichiometry of the North Sea and therefore the nutrients limiting the primary production of these waters.
- The second aim is to investigate how observed shifts in resource limitation and nutrient stoichiometry may have influenced the species and biochemical composition of phytoplankton communities in the North Sea.
- The third aim is to use the North Sea phytoplankton as a model system to contribute to an improved conceptual understanding of how competition between species affects the species composition of natural communities.

Nutrient limitation of the North Sea was investigated on multiple research cruises with the RV *Pelagia* along a transect which incorporated the nearshore region and extended to the central region (Chapter 2). Analysis of dissolved inorganic nutrients revealed a clear gradient from exceptionally high N:P ratios in the nearshore to low N:P ratios in the central North Sea. The presence of such



high N:P ratios is indicative of P limitation, which is counter to traditional expectations that the productivity of marine ecosystems tends to be N limited. The same stoichiometric gradient was observed in the seston (=phytoplankton and detritus) of the North Sea, which also showed extremely high N:P and C:P ratios in the coastal waters and much lower values in the central North Sea (Chapter 2).

Nutrient enrichment bioassays performed on board of the research vessel confirmed this spatial gradient in nutrient limitation (Chapter 2). Overall, phytoplankton growth in the nearshore region was limited by P, which transitioned to N and P co-limitation further offshore, and to N limitation in the central North Sea. Diatoms in the coastal waters were co-limited by silicate and P, while dinoflagellates and nanoflagellates including many mixotrophic species were co-limited by N and P. The different species responses indicated that further reductions of riverine P loads without concomitant reductions of N loads are likely to further suppress nuisance *Phaeocystis* blooms, but might be less effective in diminishing harmful algal blooms by dinoflagellates. The potential problems that can be caused by harmful algal blooms are illustrated by a highly toxic *Alexandrium ostenfeldii* bloom that caused major water quality issues in Zeeland in 2012 (Chapter 6).

Controlled laboratory experiments were utilized to investigate how changes in nutrient limitation would affect the species composition of phytoplankton communities collected from the North Sea (Chapter 3). Classic resource competition theory predicts that changes in nutrient ratios will alter the phytoplankton species composition. The nutrient-load hypothesis extends this classic theory, and predicts that decreasing nutrient loads will also alter the species composition even if nutrient ratios would stay the same, by shifting the species interactions from competition for light to competition for nutrients. Seven chemostats, each with a unique combination of N and P loads, were used to test these predictions. The results showed that both changes in N:P ratios and changes in absolute nutrient loads affected the phytoplankton species composition, in agreement with the theoretical predictions. However, we found a higher species diversity in the experiments than predicted by theory. This may be explained by neutral coexistence of the species, or by differences in pigment composition between diatoms, chlorophytes and cyanobacteria allowing a subtle

form of niche differentiation in which species utilize different portions of the underwater light spectrum.

To better understand how the biochemical composition of phytoplankton is impacted by changes in nutrient limitation, the phytoplankton communities grown in the experiments of Chapter 3 were further analyzed for biomolecule composition and synthesis (Chapter 4). The stable isotope  $^{13}\text{C}$  was added to steady-state communities from the chemostat experiments and incorporation of  $^{13}\text{C}$  into key biomolecules such as amino acids, carbohydrates and fatty acids was investigated. Nitrogen limitation reduced the amino acid content of the cells, and decreased the transformation from non-essential to essential amino acids, when compared to P- or light limitation. The cellular content of glucose, a storage carbohydrate, increased with nitrogen limitation, while structural carbohydrates and structural fatty acids did not vary significantly. P-limitation did not appear to impact amino acid content. The experiments had insufficient biomass for the analysis of  $^{13}\text{C}$  in nucleic acids, but it is well known from other studies that P-limitation suppresses the RNA content of cells. These changes in biomolecule composition may affect phytoplankton growth, and are a major determinant of their nutritional quality for higher trophic levels in the food web (Chapter 4).

Niche-based models and the neutral theory of biodiversity differ in their predictions of how phytoplankton communities will respond to changing nutrient loads. In particular, niche-based models assume that interspecific differences in the utilization of nutrients and light cause changes in species composition, whereas neutral theory assumes that species are equal competitors resulting in random drift of the species. To distinguish between these two fundamentally different conceptual frameworks, additional chemostat experiments were performed using natural phytoplankton collected from the North Sea. Coexistence of two species, the picocyanobacterium *Cyanobium* sp. and nano-eukaryote *Nannochloropsis* sp., occurred under P-limiting conditions. Both species were isolated and grown in monoculture to parameterize their growth kinetics. This revealed a nearly equal competitive ability for P, indicative of neutral coexistence of the two species. However, instead of the random drift predicted by neutral theory, pairwise competition experiments showed that the species abundances converged to the same steady state even if the species started from different initial conditions. Again, differences in pigment composition between the species may have played a role. That is, subtle niche differentiation

in the light spectrum may have stabilized the otherwise neutral competition for P, resulting in stable coexistence of the two species.

Overall, the impact of changing nitrogen and phosphorus loads on the phytoplankton community of the North Sea has been substantial. The more effective reduction of the P loads has resulted in P limitation of coastal waters, and an offshore gradient from P to N limitation that is reflected in both the C:N:P stoichiometry of the seston and in the growth response of the phytoplankton (Chapter 2). Furthermore, controlled experiments show that changes in both N:P ratios and total nutrient loads alter the biochemical and species composition of phytoplankton communities, and that these changes in species composition can best be described by niche-based models such as the nutrient-load hypothesis (Chapter 3, 4, 5). Further work is required to understand how higher trophic levels in the food web may be impacted by the low nutritional quality of P-limited phytoplankton. This work supports calls for continued and improved monitoring of the North Sea. Furthermore, this research demonstrates that future de-eutrophication efforts in any aquatic system should be done with balanced reductions of N and P as a core tenet

## Samenvatting

### **Een zee van verandering:**

#### ***Effecten van de afname in stikstof- en fosfaatbelasting op het fytoplankton in kustwater***

De hoeveelheid voedingsstoffen die de Noordzee en andere kustwateren instromen wordt sterk beïnvloed door menselijke activiteiten. Gedurende meerdere decennia nam de nutriëntenbelasting geleidelijk toe, wat uiteindelijk resulteerde in eutrofiëring van mariene kustecosystemen. Om de negatieve effecten van eutrofiëring een halt toe te roepen werd in 1986 in internationaal verband afgesproken om de hoeveelheid stikstof en fosfaat die via Europese rivieren de Noordzee instroomt te halveren. In de beginjaren 2000 was de totale afname van de fosfaatbelasting, met 50-70%, succesvoller dan de totale afname van de stikstofbelasting, met zo'n 20-30%. Deze onbalans in de afname van deze twee belangrijke voedingsstoffen zou kunnen leiden tot verschuivingen in de productiviteit, soortensamenstelling en voedingswaarde van marien fytoplankton aan de basis van het mariene voedselweb. Om beter te begrijpen of en hoe deze verschuiving in de nutriëntenbelasting het fytoplankton in de Noordzee heeft beïnvloed, heeft dit proefschrift zich gericht op de volgende drie doelstellingen:

- Het eerste doel is om vast te stellen of deze meerjarige verandering in de nutriëntenbelasting de verhouding van de nutriëntenconcentraties in de Noordzee heeft veranderd, en of dat heeft geleid tot veranderingen in de nutriënten die limiterend zijn voor de primaire productie van de Noordzee.
- Het tweede doel is om te onderzoeken hoe deze verschuivingen in nutriënt limitatie de soortensamenstelling en biochemische samenstelling van het fytoplankton in de Noordzee zouden kunnen beïnvloeden.
- Het derde doel is om het fytoplankton van de Noordzee te gebruiken als een model systeem voor een beter fundamenteel begrip van de effecten van concurrentie tussen soorten op de soortensamenstelling van ecosystemen.

Nutriënt limitatie in de Noordzee werd onderzocht door meerdere vaartochten met het onderzoekschip *RV Pelagia* langs een transect van de

kustzone naar het midden van de Noordzee (Hoofdstuk 2). Analyse van opgeloste anorganische nutriënten maakte een duidelijke gradiënt zichtbaar van exceptioneel hoge N:P ratio's in het kustwater tot lage N:P ratio's in het midden van de Noordzee. De aanwezigheid van zulke hoge N:P ratio's is een aanwijzing voor fosfaat (P) limitatie, en staat haaks op de traditionele gedachte dat de productiviteit van mariene ecosystemen vooral door stikstof wordt gelimiteerd. Dezelfde gradiënt is echter ook aanwezig in het seston (=fytoplankton en detritus) van de Noordzee, waarbij we ook bijzonder hoge N:P en C:P ratio's in het seston van de kustzone vonden en veel lagere waarden in de centrale Noordzee (Hoofdstuk 2).

De ruimtelijke gradiënt in nutriënt limitatie werd bevestigd door bioassays met nutriëntenbemesting aan boord van het onderzoekschip (Hoofdstuk 2). De groei van het fytoplankton in de kustzone werd gelimiteerd door P, er was een overgangszone met co-limitatie van N en P verder uit de kust, en N was limiterend in de centrale Noordzee. Diatomeeën in het kustwater werden ge-co-limiteerd door silicaat en P, terwijl bij dinoflagellaten en nanoflagellaten waaronder veel mixotrofe soorten sprake was van co-limitatie door N en P. De verschillende manieren waarop verschillende soorten reageerden gaven aan dat verdere afname van de fosfaatbelasting zonder gelijktijdige afname van de stikstofbelasting waarschijnlijk zal leiden tot een verdere terugloop van de overlast veroorzakende schuimalg *Phaeocystis*, maar minder effectief zal zijn in het beperken van schadelijke algengroei door dinoflagellaten. Dat dinoflagellaten kunnen leiden tot schadelijke algengroei met grote problemen voor de waterkwaliteit wordt goed geïllustreerd door de bloei van de bijzonder giftige *Alexandrium ostenfeldii* in de provincie Zeeland in 2012 (Hoofdstuk 6).

Hoe verschuivingen in nutriënt limitatie de soortensamenstelling van fytoplankton in de Noordzee kunnen beïnvloeden, werd onderzocht in gecontroleerde laboratorium experimenten (Hoofdstuk 3). De klassieke resource competitie theorie voorspelt dat veranderingen in nutriënt ratio's zullen leiden tot veranderingen in de fytoplankton soortensamenstelling. De nutriëntenbelasting hypothese is een uitbreiding van deze klassieke theorie, die voorspelt dat een afname van de nutriëntenbelasting ook zal leiden tot veranderingen in de soortensamenstelling als de nutriënt ratio's hetzelfde blijven, doordat de interactie tussen soorten verschuift van competitie om licht naar competitie om nutriënten. Zeven chemostaat experimenten, met elk een unieke

combinatie van stikstof- en fosfaatbelasting, werden uitgevoerd om deze voorspellingen te testen. De resultaten tonen aan dat zowel veranderingen in N:P ratio's als veranderingen in totale nutriëntenbelasting effect hebben op de fytoplankton soortensamenstelling, in overeenstemming met de theoretische voorspellingen. We vonden echter een grotere diversiteit aan soorten dan was voorspeld door de theorie. Deze hoge diversiteit kan worden toegeschreven aan neutrale coëxistentie van de soorten, of aan verschillen in pigmentsamenstelling tussen diatomeeën, groenalgen en cyanobacteriën die een subtiele vorm van niche differentiatie mogelijk maken waarbij soorten gebruik maken van verschillende delen van het onderwater lichtspectrum.

Om beter te begrijpen hoe de biochemische samenstelling van fytoplankton wordt beïnvloed door veranderingen in nutriënt limitatie hebben we de biomoleculen van het fytoplankton in de experimenten van Hoofdstuk 3 nader geanalyseerd (Hoofdstuk 4). Hiertoe voegden we de stabiele  $^{13}\text{C}$  isotoop toe aan fytoplankton uit de chemostaat experimenten en analyseerden we de opname van het toegevoegde  $^{13}\text{C}$  in belangrijke biomoleculen zoals aminozuren, koolhydraten en vetzuren. Stikstof limitatie leidde tot een afname van het aminozuur gehalte van de cellen, en afname van de omzetting van niet-essentiële naar essentiële aminozuren, in vergelijking met fosfaat- of licht limitatie. Het glucose gehalte van de cellen, voor opslag van koolhydraten, nam juist toe bij stikstof limitatie, terwijl structurele koolhydraten en vetzuren niet significant varieerden met het type nutriënt limitatie. Fosfaat limitatie bleek geen impact te hebben op het aminozuur gehalte. We hadden onvoldoende biomassa beschikbaar voor de analyse van  $^{13}\text{C}$  in nucleïne-zuren, maar het is bekend van andere studies dat P limitatie het RNA gehalte van cellen verlaagd. Deze veranderingen in biochemische samenstelling kunnen een effect hebben op fytoplankton groei, en zijn bepalend voor de voedingswaarde van fytoplankton voor hogere trofische niveau's in het voedselweb (Hoofdstuk 4).

Niche-gebaseerde modellen en de neutrale theorie voor biodiversiteit verschillen in hun voorspelling hoe de fytoplankton samenstelling zal reageren op veranderingen in de nutriëntenbelasting. Het uitgangspunt van niche-gebaseerde modellen is dat verschillen tussen soorten in hun concurrentiestrijd om nutriënten en licht leiden tot veranderingen in de soortensamenstelling, terwijl de neutrale theorie berust op de aanname dat alle soorten gelijkwaardige concurrenten zijn wat resulteert in random verschuivingen in de

soortensamenstelling. Om vast te stellen welke van deze twee fundamenteel verschillende uitgangspunten het beste van toepassing is, hebben we een nieuwe reeks van chemostaat experimenten uitgevoerd met natuurlijk fytoplankton uit de Noordzee. P limitatie leidde tot de coëxistentie van twee soorten, de picocyanobacterie *Cyanobium* en de nano-eukaryoot *Nannochloropsis*. Beide soorten werden geïsoleerd en opgekweekt in monocultuur om hun groei-eigenschappen te meten. Hieruit bleek dat de twee soorten een vergelijkbare concurrentiekracht hebben voor fosfaat, wat een indicatie is dat competitie tussen deze soorten zou kunnen leiden tot neutrale coëxistentie. Echter, in plaats van random fluctuaties te vertonen, convergeerden de beide soorten in competitie experimenten tot dezelfde stabiele evenwichts-verhoudingen ongeacht met welke initiële hoeveelheden de beide soorten het experiment begonnen. Opnieuw lijken verschillen in pigmentsamenstelling van de soorten een rol te hebben gespeeld. Dat wil zeggen, subtiele niche differentiatie in het licht spectrum heeft waarschijnlijk geleid tot stabilisering van de anderszins neutrale concurrentiestrijd, resulterend in stabiele coëxistentie van de twee soorten.

Samenvattend zijn de veranderingen in de stikstof- en fosfaatbelasting van grote invloed geweest op het fytoplankton van de Noordzee. De sterke afname van de fosfaatbelasting heeft geleid tot P limitatie van het kustwater, en een gradiënt van P limitatie bij de kust tot N limitatie in de centrale Noordzee die tot uitdrukking komt in zowel de C:N:P verhoudingen als de groei response van het fytoplankton (Hoofdstuk 2). Voorts blijkt uit laboratorium experimenten dat veranderingen in zowel N:P ratio's als totale nutriëntenbelasting leiden tot verschuivingen in de biochemische samenstelling en soortensamenstelling van het fytoplankton, waarbij verschuivingen in de soortensamenstelling het meest adequaat worden beschreven door niche-gebaseerde modellen zoals de nutriëntenbelasting hypothese (Hoofdstukken 3-5). Verder onderzoek is noodzakelijk om beter te begrijpen hoe de hogere trofische niveau's in het mariene voedselweb worden beïnvloed door de lage voedselwaarde van P-gelimiteerd fytoplankton. Dit werk onderstreept het belang van een betere monitoring van (de veranderingen in) de Noordzee. Bovendien laat dit onderzoek zien dat verdere inspanningen tot de-eutrofiëring van aquatisch ecosystemen zouden moeten berusten op gebalanceerde reducties van N en P als leidend principe.

## **Author Contributions**

**Chapter 2:** AB, MS and JH designed the study; AB, MS and LA performed field work; CPDB supervised research cruises; AB and LA analysed the samples; AB, MS and JH performed data analysis and interpretation; AB, MS, and JH wrote the manuscript, all authors commented on the final version.

**Chapter 3:** AB, MS and JH designed the study; AB, MS, EG and JG performed the field and lab work; AB and EG analysed the samples; AB, MS and JH performed the data analysis and interpretation; AB and JH wrote the manuscript, and all available authors commented on the final version.

**Chapter 4:** JG and AB designed research; MS, JH and HTSB supervised design and implementation; JG and AB performed research and data analysis; JG, AB, MS, JH and HTSB interpreted the data and wrote the manuscript.

**Chapter 5:** AB, MS and JH designed the study; AB performed the field work; AB and LM performed the lab work; AB and LM analysed the samples; AB, MS and JH performed data analysis and interpretation; AB and JH wrote the manuscript; and all available authors commented on the final version.

**Chapter 6:** AB, HCPM, RT and JH designed the study; AB, HCPM and PMV performed the lab experiments; HCPM, PMV, WdB, RT, KS, YvS and JH coordinated the field treatment; AB, HCPM, WdB, PMV and MS collected field samples; AB, PMV and HCPM analysed the phytoplankton samples; WdB analysed the macrophyte/fauna samples; RH and AG analysed the toxin samples; AB, HCPM, PMV, WdB, RT and JH wrote the manuscript and all authors commented on the final version.



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## Curriculum Vitae

Amanda Merle Burson was born on the 6<sup>th</sup> of January, 1985 in Phoenix, Arizona, USA. After completing highschool at University Highschool in Tucson, Arizona in 2003, Amanda went to Stony Brook University in New York for her undergraduate and master's degrees. She finished with Cum Laude honors with a BSc in Marine and Atmospheric Sciences in 2007. She then completed a MSc in Marine and Atmospheric Sciences in 2009 with a thesis entitled "The role of nitrogenous nutrients in the occurrence of the harmful dinoflagellate blooms caused by *Cochlodinium polykrikoides* in Long Island estuaries (NY, USA)." Her master's research was performed in the laboratory of Prof. Christopher Gobler on the bays and estuaries of eastern Long Island, New York. After completing her master's degree, Amanda moved to Galway, Ireland and worked at the Marine Institute on a project investigating the recently discovered toxic phytoplankton species *Azadinium spinosum*. She began her PhD at the University of Amsterdam in 2011 investigating the impacts of changing nutrient loads on the phytoplankton community of the North Sea. The work of this PhD is described in this thesis and this, as well as in many previous projects, have resulted in several publications.

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