Kiel, 11.8.2015

Dear Gerhard,

Herewith, I would like to submit the revised version of the manuscript, 'Effects of varied nitrate and phosphate supply on polysaccharidic and proteinaceous gel particle production during tropical phytoplankton bloom experiments '. We are thankful to the two referees, who thoroughly evaluated the manuscript and gave valuable and very detailed suggestions for improvements. We are confident to have satisfactorily addressed all major comments, and hope that the revision will meet with yours and the referee's approval.

Best regards,

Anja

Response to referees

Anonymous Referee #1:

General comments: This paper addresses an interesting issue, i.e. what will be the effects of varied nutrient supply and stoichiometry on the production and dynamics of gel particles. While I find the question interesting and the paper well written, I find the rational to justify such a study rather weak. The first sentence of the abstract suggests that "oxygen minimum zone (OMZ) will expand in the tropical oceans as a result of global change with potential consequences for marine element cycling, resulting in a lower supply of nitrate relative to phosphate". However, neither the Introduction nor the Discussion develop this argument, and the link between OMZ/global change/nutrient supply is rapidly lost, which leaves the reader with the question: What happens for gel particles if the nutrient availability is altered? Instead, the Introduction develops on the general role of inorganic nutrient availability on ecosystem productivity. It would certainly be beneficial for the paper to focus the Introduction on the expected alteration of the nutrient input/stoichiometry/cycling in OMZ, and in particular in the studied site and in the context of global change. If the link with global change and OMZ is kept in the Abstract, it also seems necessary to discuss the impact of changing nutrient availability on the long term perspective (global change) and for this specific environment (OMZ). I find the main conclusion, i.e. increasing inorganic N supply (relative to inorganic P) favors gel particles formation, rather convincing despite the limitation of the mesocosm approach to extrapolate to long term responses of natural systems (already acknowledged by the authors on page 6610).

Response: We agree with the referee that the impact of altered nutrient concentration and stoichiometry should be discussed more extensively with respect to biogeochemical consequences of oxygen minimum zones. We will expand the link between nutrients and sub/anoxia in the introduction (e.g. sinks of NO_3, sources of PO_4) and give a perspective on potential consequences for gel particles production in the discussion section.

Referee: Specific comments/questions Page 6594, Line 20: A mesh to filter out zooplankton was not used. Do you mean "was used"?

Response: A mesh was not used in order to avoid changes of the community composition tested, compared to the natural situation.

Referee: Page 6596, Line 21: The microscopic study of gel particles was conducted at a 200xmagnification. Although this magnification covers most of the gel size spectra (at least for TEP), it is probably too high to allow a good statistical determination of large particles (that are less abundant), and it probably renders the observation of small micrometric particles very difficult. This limitation is somehow acknowledged by the authors since in Fig. 5, the regression line is fitted to the data only until 14.14 µm, suggesting that above this size, the large particles are not well represented. I think this limitation should be acknowledged in the paper.

Response: Gel particles were determined in the size range 1-760 µm. We choose to fit the size distribution line to a largest size of 14.14µm ESD to assure a minimum number of 10 ml^{-1} in all samples (TEP and CSP at all time points, throughout the study) for better comparability. Larger gel particles were too seldom and variable to meet this criteria and thus would not allow for a good fit. We will include this explanation in the method section. Larger TEP thus were included in the enumeration but not in determination of the size distribution.

Referee: Page 6612, Lines 24-29: It is suggested that the high [TEP-C]:[POC] ratio is due to an underestimation of POC due to TEP passing through GF/F filters. While this possibility exists, it should also be mentioned that TEP-C could be overestimated using the TEP-C versus TEP size relationship. Indeed, the use of this relationship is very sensitive to the determination of the TEP size distribution, and one could argue that the determination of the TEP size spectra at a single x200 magnification does not allow such an accurate description of their distribution. Furthermore, this relationship has been established from phytoplankton cultures and could overestimate TEP-C of naturally occurring TEP particles.

Response: The referee raises valid arguments and we will include this potential bias of the TEP-C calculations in the discussion.

Referee: Page 6609, Lines 22-27: This paragraph brings to light the possible impact of various nutrient supply for the phytoplankton community composition. Since phytoplankton composition strongly influences the release rate and composition of TEP precursors (and probably also that of CSP), it would be useful to mention some results from the phytoplankton composition (if available). If the community composition differs significantly between treatments, the effects of changing nutrients supply and stoichiometry on the dynamics of gel particles could be only due to phytoplankton composition.
Response: Unfortunately, we do not have data to test for community differences among mesocosms. We refer to the study of Meyer et al. (2015, BGD, doi:10.5194/bgd-12-9991-2015), who describe development of cyanobacterial (nifH gene and transcript abundances) communities over time.

Referee: References The following references are listed, but are not cited in the text: - Azam and Long 2001 - Carlson 2002 - Engel et al. 2014 - Finkel et al. 2010 - Graziano et al. 1996 - Kreus et al. 2014 - Mills et al. 2004 - Moore et al. 2008
The following references are cited, but are not in the reference list: - Fraga 2001 - Hauss et al. 2012 - del Giorgio and Duarte 2002 - Chin et al. 1998 - Verdugo et al. 2004 - Hauss et al. 2013 - Meyeret al. 2015 - Berman and Viner-Mozzini 2001 - Claquin et al. 2008 - Underwood etal. 2004 - Alldredge et al. 1995 - Arrigo 2005
The following references are not cited properly: - Rhee 1974 or 1978? - Fogg 1966 or 1983? - Bakker et al. 2007 or Baker et al. 2007? - Logan et al. 1995 or 1994?
Response: We thank the referee for carefully checking the references. We will correct the list during revision.

Anonymous Referee #2
Specific comments: Comments by reviewer #1 also reflect my concerns. In particular, I would like to see some information given on the phytoplankton community composition.
Response: The species composition of the phytoplankton communities was not assessed quantitatively. However, we did not notice obvious differences between mesocosm of each experiment. Small initial differences with respect to the cyanobacterial population were determined and are included in Meyer et al (2015, BGD doi:10.5194/bgd-12-9991-2015).

P6594 L17: Already stated by anonymous reviewer #1: a mesh was used I presume? What size was the mesh and if no mesh was used, what is the reasoning behind this, as this would have serious consequences for these mesocosm experiments.
Response: A mesh was not used in order to avoid changes of the community composition tested, compared to the natural situation. Moreover, cells may break during mesh filtration, which would potential lead to higher DOM release and bias gel particles formation.

P6594 L23: So only one beaker was taken from which all subsamples for the various analyses were obtained? What volume did the beaker have? Also where was this sampled i.e. was it thus only surface water? Was the water in the tank mixed before sampling? Please clarify this for the reader. This would have an impact on how representative the sample is. If there was any mixing then this would have had to be very gentle to not influence gel particle formation, etc., so I presume there wasn't any? The depth of sampling would also affect gel particle abundance since it can be expected that particles will potentially settle out as they aggregate and bloom dynamics change.
Response: The beaker had a 10 L volume and 5.5-7 liter were sampled from each mesocosm at the surface. The mesocosms were gently mixed prior to sampling to obtain representative samples for the entire mesocosm. We will add this information to the manuscript.

P6590 L6ff: I suggest to exclude the description of TEP and CSP from here: "Here, were investigated how different ... affect the abundance and size distribution of polysaccharidic transparent exopolymer particles (TEP) and proteinaceous Coomassie stainable particles (CSP)." The phrase "which are suggested to enhance particle aggregation and export fluxes" could also be applicable to CSP and it is unclear why only CSP would be a "supposedly" good substrate for heterotrophic bacteria and not also TEP.
Response: We altered the abstract to include both TEP and CSP for aggregation and microbial cycling proccesses

P6592 L10: Perhaps write: "To date, mostly two types of gel particles have been studied in seawater:
...
" Since other gel particles have also been 'described' or at least suggested to be present in seawater
...
Response: Adopted

P6596 L11ff and 18ff: Why do you mention that a certain number of tanks was similar or smaller in ratios to the Redfield value, whilst for the other you mention those that had a larger ratio? What is the rationale behind this?
Response: The rationale was to indicate in how many mesocosms of Varied P the conditions were supposedly non- P limiting (N:P< or equal to 16) and in how many mesocosms during Varied N the conditions were supposedly non- N limiting (N:P> or equal to 16).

P6600 L9: You refer here to there also being a higher variability in the varied N experiment, however, you also have a higher number of different treatments compared to the P experiment.
Response. We had 15 mesocosms in Varied P and 17 mesocosms in Varied N. However, the variability in Chl a concentration was much higher in Varied N, even if we exclude the highest and lowest values in Varied N. So we think that the notice of higher variability in Varied N is valid.

P6606 L9: Perhaps it would be good to also include a similar figure as Fig. 5 for CSP.
Response: We modified the figure to include CSP size distributions

P6607 L5: You mention you relate the gel particle abundance to bloom development but in fact you mostly only relate it to the period until day 6 and thus exclude the bloom decline. In addition you have no data for 3 and 4, which should be acknowledged somewhat when interpretations are being made. You also mention in the next part that abundances were related to chl a until the bloom peak, however, the bloom peak for Varied P was on day 5 and large changes in the biogeochemistry have already happened on day 6 in these mesocosms.
Response: We modified this sentence to **'**In order to identify differences between the two series of mesocosms experiments, gel particle abundance was compared to bloom development, which also differed between the experiments.' In the following, we related gel particles to organic matter production for the full period and to Chl a concentration until the bloom peak (day 5 for Varied P and day 6 for Varied N). We added this information to the figure caption.

P6614 L9: I may have not understood correctly but is it really new formation of CSP or CSP potentially disaggregating? You mention only a few sentences later that CSP numbers decreased at the end of Varied N with a potentially higher loss than new formation.
Response: We revised this paragraph to clarify that CSP new formation was observed during the bloom and post-bloom periods. A decrease in total number and area of CSP was observed only at the last day (day 8) of Varied N. We suggest that increasing bacterial decomposition activities at that time lead to a net decrease in CSP.

Table 4 and in the main text: Why do you use Mol% for TEP-C:POC but mol:mol for TEP-C:PN?
Response: We use Mol% when the reference element is the same (C:C) and Mol:Mol when the elements are different (C:N).

Unclear sentences/phrases are the following lines, which either do not make sense as they currently stand or do not fully explain what aspects are meant, and would require reworking:
P6591 L12-16, in particular the last part does not fit well. Why also a new paragraph here? The next sentence is also unclear (L16-21).
Response: This is referring to the following sentences: 'Growth strategies relying on specific cellular nutrient requirements were also suggested to induce non-Redfield stoichiometry in oceanic biomass (Klausmeier et al., 2004; Mills and Arrigo, 2010; Franz et al. 2012b) and changes in community structure have been reported as response to changes in nutrient ratios (Sommer et. al., 2004; Hauss et al., 2012). With regard to CO2 uptake and organic matter production, variations in element stoichiometry have been linked to carbon overconsumption - a particular increase in carbon assimilation relative to the uptake of nitrogen and phosphorous (Toggweiler, 1993; Schartau et al., 2007), when photosynthesis proceeds, while cell division and growth are hampered due to nutrient limitation (Wood and van Valen, 1990).'
These sentences explain that cells have different requirements for C, N, and P, which is seen in biomass and also by changes in species composition when nutrient ratios changes. The sentence 16-21 explains how carbon overconsumption affects carbon to nutrient ratios.

P6608 L12: thereby – not the right word to use here.
Response: We exchanged 'thereby' with 'the'

P6608 L28: what factors? Which factors do you refer to here?
Response: We can only speculate about these factors as the treatment of these mesocosms was the same during the two experiments. We therefore removed this sentence from the results section and added to the discussion that differences in initial community structures such as described in Meyer et al. may have co-affected the nutrient treatment.

P6609 L17-21, especially the last part.
P6609 L26 - P6610 L4
P6610 L10-14: what is meant by 'potential variability of ecological responses towards nutrient supply'? What ecological variability??
P6612 L13-15: may contrasts??
P6615 L2-3
Response: We reformulated the sentence to clarify the point.

Technical corrections: - Please make sure that throughout the document coomassie stainable particles is in fact written as Coomassie stainable particles i.e. Coomassie with a capital letter.
Throughout please make sure you use “gel particle” when written together with other words such as ‘gel particle formation’, ‘gel particle abundance’ and not gel particles abundance or gel-particles abundance. Only if ‘gel particles’ is used on its own and the plural is meant do you write it with an -s.
Response: Adopted

Abstract: L7: we investigated how
L14: In the days until the bloom peak is reached, a positive correlation ...
L17: After the bloom peak,
Response: All adopted

Introduction: P6591 L16ff: Add onto previous paragraph, not a new paragraph. Separate paragraphs later in line 21.
Response: Adopted

P6591 L22: in the form of dissolved
Response: Adopted

...
P6592 L8: Verdugo et al., 2004). ->Begin a new paragraph here. “The formation of gel particles thus represents
Response: Adopted

...
”
P6592 L16: been reported ([add some newer references here]), with higher
Response: Newer reference was added
...
P6592 L17: It has been shown that the rate
P6593 L12: nitrogen in the form of CSP thus represents
important source of nutrition.

Response: All adopted

P6595 L5:
(Table 1) for 14 tanks. Two additional
Response: Adopted 'for 13 tanks'

P6596 L3: Samples for the dissolved
P6596 L5: is it really Quaatro? Perhaps Quattro?
Section 2.2.1.: Please specify what volume of sample was used for these analyses.
P6596 L10: Please specify at least for how long the staining was done.
P6598 L7: the range found in samples were prepared
P6599 L5: HCl not HCL
P6599 L10: experiments were statistically tested
P6600 L12: response was much stronger
P6600 L15, 19: mesocosm; also check other places where 'mesocosms' is in combination with 'experiment' or other words and should be 'mesocosm' instead.
P6603 L7: initial (day 1) TEP numerical
P6605 L17: at the end of the experiment.
P6606 L3: the figure reference (Fig 6b, left) is incorrect:
P6606 L20: Multiple comparison (Holm-Sidak) tests revealed
P6607 L18: the figure reference (Fig 8b-f) is incorrect:
P6608 L27: the increase in CSP abundance over time
P6609 L7: in a large variation
P6609 L24: remove superfluous comma after days.
P6610 L8: to long-term responses of natural
P6610 L18: Chow et al. (wrong by Marine Chemistry but how it will be cited)
P6610 L23: influencing this release
P6611 L12: In addition, phosphorus
P6611 L25: North Pacific (offshore Hawaii).
P6612 L15: bloom build-up and decay.
P6612 L21: to the POC pool in the form of TEP.
accounted for 0.5µMol C (initial days) to
P6613 L13: about the role of CSP on the organic carbon and, more importantly, on organic
P6613 L15: for auto- and heterotrophic growth. During this study [also no new paragraph here]
P6613 L21: at a later time. Because
P6614 L14: accordance with findings
P6615 L4: Particle dynamics of TEP and CSP differ..

Response: All adopted!

Effects of varied nitrate and phosphate supply on polysaccharidic and proteinaceous gel particles production during tropical phytoplankton bloom experiments

Engel, A., Borchard, C., Loginova, A., Meyer, J., Hauss, H. and Kiko, R.

GEOMAR Helmholtz Centre for Ocean Research, 24105 Kiel, Germany

Keywords: Transparent exopolymer particles (TEP), Coomassie stainable particles (CSP), mesocosms, N:P ratio, dissolved organic carbon (DOC), dissolved organic nitrogen (DON)

Abstract

It has been suggested that oxygen minimum zones (OMZ) will expand in the T~~t~~ropical O~~o~~ceans as a result of global change with potential consequences for marine element cycling, such as an increase in anaerobic nitrogen loss, resulting in a lower supply of nitrate relative to phosphate to the euphotic zone. So far, the effects of changes in nutrient ratios on organic matter recycling and export fluxes are not well understood. Here, we~~re~~ report of two series of mesocosm experiments that were conducted to investigated how different phosphate (Experiment 1, *Varied P:* 0.15 - 1.58 µmol L^{-1}) or nitrate (Experiment 2, *Varied N:* 1.9 - 21.9 µmol L^{-1}) concentrations affect the abundance and size distribution of polysaccharidic transparent exopolymer particles (TEP), and of proteinaceous Coomassie stainable particles (CSP). Both types of gel particles ~~which are~~ play an important role in biogeochemical and ecological processes like ~~suggested to enhance~~ particle aggregation and export ~~fluxes~~, ~~and on proteinaceous coomassie stainable particles (CSP), a supposedly~~ organic substrate ~~for~~ microbial nutrition and growth ~~heterotrophic bacteria~~. ~~Two~~ The~~series of mesocosm bloom~~ experiments were conducted with natural plankton communities collected from the Eastern Tropical North Atlantic (ETNA) close to Cape Verde in October 2012. In the days ~~U~~until the bloom peak was reached, a positive correlation between gel particle abundance and Chl *a* concentration was determined, linking the release of dissolved gel precursors and the subsequent formation of gel particles to autotrophic production. After the bloom peak, gel particle abundance remained stable or even increased, implying a continued partitioning of dissolved into particulate organic matter after biomass production itself ceased. During both experiments, differences between TEP and CSP dynamics were observed; TEP were generally more abundant than CSP. Changes in size distribution indicated aggregation of TEP ~~during~~ after the bloom, while newly formed CSP decomposed. Abundance of gel particles clearly increased with nitrate concentration during the second experiment, suggesting that changes in

[DIN]:[DIP] ratios can affect gel particle formation with potential consequences for carbon and nitrogen cycling as well as food web dynamics in tropical ecosystems.

1. Introduction

Ecosystem productivity in the surface ocean is largely controlled by the availability of inorganic nutrients. The Redfield ratio describes a constant molar ratio of C:N:P of 106:16:1 and associates the relative elemental composition of seawater to that of marine organisms (Redfield, 1958;~~,~~ Redfield et al., 1963). It provides a widely used basis for the calculation of elemental fluxes in marine food webs and biogeochemical cycles~~.~~ (Sarmiento and Gruber, 2006;~~,~~ Sterner and Elser, 2002). On a regional or temporal scale, however, strong deviations of cellular composition from the Redfield ratio were reported (Fraga, 2001; Geider and LaRoche, 2002)~~.~~ ~~One reason is~~ and related to the physiological state of cells ~~of individual primary producers or communities, which was shown to affect elemental composition~~ (Rhee, et al. 19787~~4~~; Goldman et al., 1979; Falkowski, 2000; Borchard et al., 2011; Franz et al., 2012a), differences in~~.~~ g~~G~~rowth strategies ~~relying on specific cellular nutrient requirements were also suggested to induce non Redfield stoichiometry in oceanic biomass~~ (Klausmeier et al., 2004; Mills and Arrigo, 2010; Franz et al. 2012b) and changes in community structure ~~have been reported as response to changes in nutrient ratios~~ (Sommer et. al., 2004; Hauss et al., 2012).

With regard to CO_2 uptake and organic matter production, variations in element stoichiometry of cells have been linked to carbon overconsumption - a particular increase in carbon assimilation relative to the uptake of nitrogen and phosphorous (Toggweiler, 1993; Schartau et al., 2007), when photosynthesis proceeds, while cell division and growth are hampered due to nutrient limitation (Wood and van Valen, 1990).

A fraction of this 'excess carbon' is released from phytoplankton cells in the form of dissolved organic carbon (DOC). DOC release occurs during all stages of phytoplankton growth (Fogg, ~~1966~~1983; Mague et al., 1980; Bjørnsen, 1988). In natural communities, the percentage of extracellular release typically ranges between 10-20% (Baines and Pace, 1991; Nagata, 2000). Depending on their nutrient status, however, marine phytoplankton cells can release up to 80% of primary production as DOC (Sharp, 1977; Mague, 1980; Fogg, 1983~~;~~ Bjørnsen, 1988). Thereby, the extent and composition of freshly produced DOC is affected by various environmental factors, such as temperature, CO_2 concentrations and nutrient supply (Thornton, 2009; Engel et al., 2011; Borchard and Engel, 2012). Abiotic factors influencing DOC production concomitantly define its fate in the global carbon cycle. DOC can either be transferred back to CO_2 by microbial degradation and respiration (Azam, 1983; Ducklow et al. 1986; del Giorgio and Duarte, 2002), or it can be transformed into particulate organic carbon (POC), either through uptake by organisms, or by abiotic assembly and coagulation into gel particles (Alldredge et al., 1993; Chin et al., 1998; Engel et al., 2004a; Verdugo et al., 2004).

The ~~F~~formation of gel particles thus represents an abiotic pathway of repartitioning dissolved organic matter (DOM) into particulate organic matter (POM). To date, mostly two types of gel particles have been described in seawater: transparent exopolymer particles (TEP) that are rich in carbon and mainly originate from dissolved polysaccharides, and C~~c~~oomassie stainable particles (CSP) that are rich in nitrogen and assumed to form from proteinaceous compounds (Alldredge et al., 1993; ~~Passow, 2002;~~ Long and Azam, 1996; Engel, 2009; Cisternas-Novoa et al., 2015). Ubiquitous in the ocean, numerical abundances of TEP and CSP around 10^6 L^{-1} have been reported, with higher abundances (10^8 L^{-1}) during phytoplankton blooms (Long and Azam, 1996;

Passow, 2002; Galgani et al., 2014). It ~~was~~ has been shown that the rate of TEP formation during phytoplankton blooms is controlled by the release rate of dissolved polysaccharides (Engel et al., 2004a). TEP abundance often increases at times when phytoplankton growth becomes nutrient limited, either by nitrogen (Corzo et al., 2000; Pedrotti et al., 2010) or by phosphorus (Borchard and Engel, 2011). In addition to phytoplankton, often considered as main source of dissolved gel precursors, bacteria can significantly contribute to the DOM pool and therewith to TEP and CSP formation (Radic et al., 2006; Vadstein et al., 2012).

TEP play an important role in the formation of particle aggregates and therewith can enhance carbon export fluxes in marine systems (Passow et al., 2001; Engel et al., 2014). Due to the high carbohydrate content, high abundance of TEP can increase C:N ratios of suspended and sinking particles in the ocean (Engel et al., 2002, Schneider et al., 2004; Schartau et al., 2007).

It has been suggested that CSP and TEP are different particles, as their spatial and temporal occurrence in the ocean can be quite different (Cisternas-Novoa et al., 2015). Compared to TEP, much less is known for processes controlling CSP formation. However, it can be assumed that dissolved precursor concentration and quality are affecting CSP formation in a similar way that DOC precursors are affecting TEP formation (Cisternas-Novoa et al., 2014). Thus, CSP formation may be part of the extracellular cycling of organic nitrogen, i.e. CSP precursors are released by microorganisms into the dissolved organic nitrogen (DON) pool and repartitioned into particles by abiotic gel particle formation. Nitrogen is often considered to be a temporarily limiting element of biomass production in marine ecosystems, favouring auto- and heterotrophic nitrogen fixation (Gruber and Sarmiento, 1997; Deutsch et al., 2007). A labile, extracellular fraction of organic nitrogen in the form of CSP thus represents a potentially important source of nutrition~~us resource~~. Moreover, extracellular particulate nitrogen included in CSP may

erroneously be attributed to the cellular nitrogen pool and may hence disguise the real nitrogen cell quota. Thus, a better knowledge on CSP formation and of the factors controlling CSP abundance may greatly improve our understanding of nitrogen cycling in marine ecosystems. So far it is unknown, how much CSP contribute to variable stoichiometry of POM, but we can expect that changes in N:P nutrient stoichiometry favouring organic nitrogen release also support higher CSP abundance, potentially increasing the nitrogen fraction in POM.

In this study, we investigated how gel particle formation is affected by different nitrate and phosphate concentrations during mesocosm bloom experiments with natural plankton communities collected from surface waters of the Eastern Tropical North Atlantic (ETNA), close to Cape Verde. At this site, surface waters are often depleted in nutrients (Hauss et al., 2013). Coastal upwelling, N_2- fixation or deposition of Aeolian dust represent prevalent pathways of nutrient, particularly inorganic nitrogen, supply to nutrient depleted surface waters (Bak~~k~~er et al., 2007; Hansell et al., 2004; Hauss et al., 2013). On the other hand, anoxic mesoscale eddies have been described recently in surface waters around Cape Verde, potentially leading to enhanced nitrogen losses (Karstensen et al., 2014). Thus, pelagic communities in the euphotic zone of the ETNA are occasionally exposed to nutrient pulses with different $[NO_3^-]$: $[PO_4^{3-}]$ ~~[DIN]:[DIP]~~ ratios in surface waters.

Understanding the impact of changes in nutrient stoichiometry on phytoplankton communities in the Tropical Ocean may also help to better estimate consequences of suboxia on ecosystem productivity and biogeochemical cycling. Coastal boundary upwelling systems in the ETNA and Eastern Tropical North Pacific (ETNP) include some of~~f~~ the largest oxygen minimum zones (OMZ) in the ocean (<20-45 µmol O_2 kg^{-1}) (Gilly et al., 2013). Although they comprise only a small fraction of the global ocean by volume, they nevertheless play a pivotal role in controlling

Formatiert: Zeilenabstand: Doppelt

Formatiert: Tiefgestellt

Formatiert: Hochgestellt

the oceans nutrient regimes (Lam and Kuypers, 2011). A profound loss of the oceanic nitrate stock was suggested to occur in OMZ's (Gruber and Sarmiento, 1997, Codispoti et al., 2001) due to microbial processes, such as heterotrophic denitrification and anaerobic ammonium oxidation (anammox) (Codispoti and Richards, 1976; Kuypers et al., 2005). As a consequence, the $[NO_3^-]$: $[PO_4^{3-}]$ stoichiometry of upwelling water masses above OMZ's with strong nitrogen loss often deviate from the canonical Redfield ratio of 16 (Deutsch et al., 2007). Because global climate change may lead to an expansion of OMZ, particularly in the Atlantic and Pacific Ocean (Stramma et al., 2008), future changes in surface ocean nutrient cycling are to be expected.

Our experiments aimed to identify effects of varied nutrient supply and stoichiometry on the abundance and size distribution of TEP and CSP, their dissolved precursors and the potential impact on carbon and nitrogen cycling.

Formatiert: Schriftart: Times New Roman, 12 Pt., Englisch (Großbritannien)

Formatiert: Schriftart: Times New Roman, 12 Pt., Englisch (Großbritannien)

Formatiert: Schriftart: Times New Roman, Englisch (Großbritannien)

2. Methods

2.1 Setup of the mesocosms

Two 8-day mesocosm experiments were conducted in October 2012 at the Instituto Nacional de Desenvolvimento das Pescas (INDP), Mindelo, Cape Verde. Surface water was collected with RV *Islândia* south of São Vicente (16°44.4'N, 25°09.4'W) using four 600L containers. Surface water was collected in the night of the 1.10.2012/2.10.2012 (first experiment) and 11.10.2012/12.10.2012 (second experiment). Sixteen mesocosm (MK) bags were placed in four flow-through water baths and shaded with blue, transparent lids to approximately 20% of surface irradiation. Mesocosm bags were filled from the containers by gravity, using a submerged hose to minimize bubbles. A mesh to filter out zooplankton was not used in order to avoid changes of the community composition as well as breakage of delicate cells. The accurate volume inside the individual bags was calculated after addition of 1.5 mmol silicate and measuring the resulting silicate concentration. The volume ranged from 106 to 145 L. In order to keep temperature constant, all MKs were evenly distributed between four water baths, the temperature of which was maintained at 25.9 - 28.7°C using water from the bay close to the experiment site. Daily sampling was conducted between 9.00 a.m. and 10.30 a.m. with a 10L beaker completely rinsed with ultra-pure water. Between 5.5 and 7 liters were sampled from each mesocosm at the surface. The mesocosms were gently mixed prior to sampling to obtain representative samples for the entire mesocosm

The experimental manipulation comprised additions of different amounts of nitrate (NO_3^-) and phosphate (PO_4^{3-}) at day 1 of the experiment. Treatment identifications specifying micromolar target concentrations of NO_3^- and PO_4^{3-} are given in table 1. Nutrient concentrations before

Formatiert: Schriftart: (Standard) Times New Roman, Englisch (USA)

Formatiert: Schriftart: (Standard) Times New Roman

nutrient addition were below the detection limit for NO_3^-, NO_2 and PO_4^{3-} while only traces of NH_4 (<0.08 µmol L^{-1}) were determined.

In the first experiment (referred to as *Varied P* in the following), the PO_4^{3-} supply was changed at constant NO_3^- supply, ~~aiming at a range of 0.25~~ yielding a range of 0.25-1.75 µmol L^{-1} PO_4^{3-} at 12.0 µmol L^{-1} NO_3^- (Table 1) for 13 tanks. Two additional MKs were set to 1.10 µmol L^{-1} PO_3^{4-} at 6.35 and 17.65 µmol L^{-1} NO_3^-, respectively, representing low and high NO_3^- treatments. One mesocosm (MK 5) received erroneous filling during the *Varied P* experiment and was excluded from data evaluation. ~~-~~Realized concentrations of PO_3^{4-} and NO_3^- inside the mesocosms slightly deviated from target values (Table 1), which may be due to fast uptake, or to underestimation of water volume. Initial $[NO_3^-]$: $[PO_4^{3-}]$~~NO_3^-: PO_4^{3-}~~ during *Varied P* covered a range of 6.7 – 77, with ratios similar to, or smaller than the Redfield value, in 11 out of 15 mesocosms, suggesting non-P-limiting conditions in the majority of mesocosms during the first experiment. ~~[DIN]:[DIP] ratios similar to, or smaller than the Redfield value in 11 out of 15 mesocosms~~.

During the second experiment (referred to as *Varied N* in the following), initial NO_3^- concentration was varied at relatively constant PO_3^{4-} concentration, yielding a target range of 2.0 - 20.0 µmol L^{-1} NO_3^- at 0.75 µmol L^{-1} PO_4^{3-} in 12 out of 16 MKs (Table 1). In addition, two low and two high PO_3^{4-} treatments at low and high NO_3^- were realized. The realized nutrient concentrations deviated only slightly from target values. $[NO_3^-]$: $[PO_4^{3-}]$~~NO_3^-: PO_4^{3-}~~ ~~ratios~~ during *Varied N* therewith covered a range of 3.3 – 84 with ratios of > 16, in 9 out of 16 mesocosms suggesting non-N-limiting conditions ~~–~~in the majority of mesocosms during the second experiment. ~~9 out of 16 mesocosms realizing [DIN]:[DIP] ratios of > 16.~~

Two nutrient treatments were realized in both experiments; 12.0N/0.75P with 4 replicates during *Varied P* and 3 replicates during *Varied N*, and 6.35N/1.10P with 1 mesocosm during each experiment.

200

201 **2.2 Analytical methods**

202 **2.2.1. Inorganic nutrient**

203 Samples (10ml) for the dissolved inorganic nutrients nitrate (NO_3^-), nitrite (NO_2^-) and phosphate
204 (PO_4^{3-}) were taken daily from each mesocosm. ~~an~~
205 ~~d~~Duplicate measurements were carried out~~d~~ within four hours after sampling using a Qua~~a~~ttro
206 Autoanalyzer according to Grasshoff et al. (1999). Detection limits of nutrients were 0.01 µmol
207 L^{-1} for NO_2^- and PO_4^{3-}, and 0.03 µmol L^{-1} for NO_3^-.
208

209 **2.2.2 Gel particles**

210 For TEP and CSP, duplicate samples of 20-80 ml were gently (< 150 mbar) filtered onto 25 mm
211 nuclepore membrane filters (0.4 µm pore size, Whatman Ltd.). Samples were stained with either
212 1ml of pre-filtered (<0.2 µm) Alcian Blue solution (Allredge et al., 1993) or 1ml of pre-filtered
213 (<0.2 µm) Coomassie Brilliant Blue solution (Long and Azam, 1996). After a staining time of
214 approximately 4s (Alcian Blue) or 30s (Coomassie Brilliant Blue), the ~~E~~excessive dye was
215 removed by rinsing the filter with several millilitres of MilliQ water. Blank filters were prepared
216 from the same MilliQ water. No samples for gel particles have been taken during *Varied P* on
217 day 3 and 4 due to a break-down of the ultra-pure water system.
218 Each filter was placed on the white side of a semi-transparent glass slide (CytoClear, Poretics
219 Corp., Livermore, US) and stored frozen (-20°C) until microscopic analysis. Abundance, area
220 and size frequency distribution of transparent exopolymer particles (TEP) and of C~~e~~oomassie
221 stainable particles (CSP) in the size range 1-760 µm were determined after Engel (2009) using a
222 light microscope (Zeiss Axio Scope A.1) connected to a camera (AxioCAM Mrc). Filters were
223 screened at 200x magnification. 30 pictures were taken randomly from each filter in two

perpendicular cross sections (15 pictures each; resolution 1040 x 1040 pixel, 8-bit color depth). Image analysis software WCIF ImageJ (Version 1.44, Public Domain, developed at the US National Institutes of Health, courtesy of Wayne Rasband, National Institute of Mental Health, Bethesda, Maryland) was used to semi-automatically analyse particle numbers and area.

The size frequency distribution of gel particles can be described by:

$$dN / d(d_p) = k d_p^{\delta} \quad (1)$$

where dN is the number of particles per unit water volume in the size range d_p to $[d_p + d(d_p)]$ with d_p being the equivalent spherical diameter (ESD), k is a constant that depends on the total number of particles per volume, and δ ($\delta < 0$) describes the spectral slope of the size distribution. The less negative δ the greater is the fraction of larger gels. Both, δ and k were derived from regressions of $\log[dN/d(d_p)]$ versus $\log[d_p]$ (Mari and Kiørboe, 1996). The value δ is related to the slope of the cumulative size distribution $N = a d_p^{\beta}$ by $\delta = \beta + 1$. To determine δ, data for CSP and TEP were fitted over the size range 1.05-14.14 µm ESD. Median size (ESD) of TEP and CSP were determined over the whole size range (1-760 µm).

The carbon content of TEP (TEP-C) was estimated after Mari (1999) using the size dependent relationship:

$$TEP\text{-}C = a \, \Sigma_i \, n_i \, r_i^D \quad (2)$$

with n_i being the number of TEP in the size class i and r_i the mean equivalent spherical radius of the size class. The constant a = 0.25 * 10^{-6} (µg C) and the fractal dimension of aggregates

247 *D*=2.55 were proposed by Mari (1999). In order to relate TEP-C to POC and TOC, data are given
248 as µmol L^{-1}.

249

250 **2.2.3 Dissolved organic carbon and nitrogen**

251 Duplicate samples for DOC (20 ml) were filtered through pre-combusted GF/F filters (450°C for
252 5 hours) and collected in pre-combusted glass ampoules (450°C for 5 hours). Samples were
253 acidified with 80 µl of 85% phosphoric acid, flame sealed and stored at 4°C in the dark until
254 analysis. DOC samples were analysed by applying the high-temperature catalytic oxidation
255 method (TOC -VCSH, Shimadzu) after Sugimura and Suzuki (1988). The instrument was
256 calibrated every 8-10 days by measuring standard solutions of 0, 500, 1000, 1500, 2500 and 5000
257 µg C L^{-1}, prepared from a potassium hydrogen phthalate standard (Merck 109017). Every
258 measurement day, ultrapure (MilliQ) water was used for setting the instrument baseline, followed
259 by the measurement of deep-sea water with known DOC concentration (Dennis Hansell,
260 RSMAS, University of Miami) to verify results. Additionally, two internal standards with DOC
261 within the range of ~~those in~~ found in samples were prepared each measurement day using a
262 potassium hydrogen phthalate (Merck 109017). DOC concentration was determined in each
263 sample from 5 to 8 injections.

264 Simultaneously with DOC, total dissolved nitrogen (TDN) was determined using the TNM-1
265 detector on the Shimadzu analyzer. Dissolved organic nitrogen (DON) was calculated from TDN
266 by subtraction of NO_3^-, NO_2 concentrations.

267

268 **2.2.4 Chlorophyll *a***

Samples (0.5-1 L) for chlorophyll a (Chl *a*) were vacuum-filtered (<200 mbar) onto Whatman GF/F filters (25mm), 1 ml of ultrapure water was added and the filters were frozen at -20°C for at least 24 hours. Subsequently, 9 ml acetone (100 %) was added to each sample and the fluorescence was measured with a Turner Trilogy fluorometer, which was calibrated with a Chl *a* standard (*Anacystis nidulans*, Walter CMP) dilution series. Chl *a* concentrations were calculated according to Parsons et al. (1984).

2.2.5 Bacterial abundance

Bacterial cell counts were obtained by flow cytometry (FACScalibur, Becton Dickinson, San Jose, CA, USA). Samples (5ml) were fixed with formaldehyde (2% final concentration), frozen at -80°C and transported to the home laboratory. Samples were diluted 1:3, stained with SYBR Green I (Molecular Probes) and measured at a flow rate of 11.0 µl min^{-1}.

2.2.6 Particulate organic carbon and nitrogen

For analyses of particulate organic carbon (POC) and particulate nitrogen (PN) water samples (0.5-1 L) were filtered onto pre-combusted (450°C for 5 hours) Whatman GF/F filters (25mm, 0.7 µm) under low pressure (<200 mbar). Filters were frozen at -20°C and stored until analysis. Prior to analysis, filters were acid fumed (37% HC~~l~~l for 24 hours) in order to remove inorganic carbon and dried at 40°C for 24 hours. Subsequently, filters were wrapped in tin cups (8 × 8 × 15 mm), combusted and analyzed according to Sharp (1974) using an elemental analyzer (Euro EA).

2.3 Data analysis

Differences in terms of nutrient manipulation and course of the experiments were statistically tested by multiple comparison (Holm-Sidak-method) or by two-way ANOVA with factors being the treatment identification (Table 1) and day of the experiment, respectively. To determine a potential effect of the nutrient treatment, the mean deviation (*MD*) of a component in a mesocosm was calculated as mean of daily deviations. Those were calculated for each sampling day by subtracting the mean value of all mesocosms at that day from the value of the individual mesocosm at the same day. For each experiment, *MD*-values were correlated to the initial (day 1) nutrient concentration. The overall significance level was $p<0.05$. Statistical tests were performed using Sigma Plot 12.0 (Systat).

3. Results

3.1 Phytoplankton bloom and nutrient development

The development of phytoplankton blooms during the mesocom experiments and the build-up of particulate matter ~~is~~ are described in more detail in Meyer et al. (2015~~*in prep.*~~) and is summarized here only briefly.

Before nutrient addition (day 0), Chl *a* concentration was on average 0.38 ± 0.09 µg L^{-1} in all mesocosms of *Varied P* and hence higher than at the start of *Varied N* with 0.18±0.05 µg L^{-1} (Table 1). As long as nutrients were replete, bloom development was similar in all mesocosms within each experiment (Fig. 1a-f). However, during *Varied P* most mesocosms reached maximum Chl *a* concentrations, i.e. bloom peak, on day 5 and thus one day earlier than during *Varied N* (Fig. 1 a, b). Maximum Chl *a* concentration ranged between 2.1 and 3.3 µg L^{-1} during *Varied P* and between 2 and 10 µg L^{-1} during *Varied N*. Hence, during *Varied N* higher concentrations of Chl *a* were determined as well as a higher variability among mesocosms. During both experiments mean deviations (MD) of Chl *a* concentration in the different mesocosms were correlated to the concentration of the initial nutrient varied, i.e. PO_4^{3-} during *Varied P* and NO_3^- during *Varied N*, although the response ~~much~~ was much stronger during *Varied N* (Table 2). The phytoplankton biomass composition was dominated by diatoms (data not shown). Diazotrophic bacteria of the genus *Trichodesmium* were more present in the initial waters of *Varied P*, while proteobacterial diazotrophs were more abundant in *Varied N* (Meyer et al., ~~*in prep.*~~2015).

Formatiert: Schriftart: Nicht Kursiv

Bacterial abundance was not determined before nutrient addition, but data from day 2 showed higher abundance in mesocosms of *Varied N* with 8.37 x 10^5 ± 9.80 x 10^4 ml^{-1} compared to 5.26x10^5 ± 5.48 x 10^4 ml^{-1} for *Varied P*. During the first four days of both experiments, cell

numbers remained relatively stable or even decreased slightly (Fig. 1 c, d). After day 5, cell numbers increased in all mesocosms and strongly differed between treatments. During *Varied P*, different PO_4^{3-} addition could not significantly explain differences in bacterial abundance (Table 2). Instead, highest abundances in the bloom phase were reached in the 'centerpoint' treatment (12.0N/0.75P), with a maximum value of $2.4x10^6 \pm 7.1x10^5$ ml^{-1} on day 6 compared to $2.3x10^6 \pm 7.1x10^5$, $1.5x10^6 \pm 3.0x10^5$ and $1.7x10^6 \pm 8.4x10^5$ ml^{-1} in treatments 12.0N/0.25P, 12.0N/1.25P and 12.0N/1.75P, respectively. During *Varied N*, bacterial abundances were positively influenced by NO_3^- input (Table 2). At the end of the experiment (day 8) $1.6x10^6 \pm 4.7x10^5$ and $2.3x10^6 \pm 5.4x10^5$ ml^{-1} cell were observed in the high NO_3^- treatments 20.0N/0.75P and 12.0/0.75P, respectively, compared to $8.1x10^5 \pm 1.4x10^5$ and $1.0x10^6 \pm 1.5x10^5$ ml^{-1} in 2.0N/0.75P and 4.0N/0.75P, respectively.

Initial concentrations of particulate organic carbon (POC) were 13.6±3.8 µmol L^{-1} and 11.9±1.9 µmol L^{-1} during *Varied P* and *Varied N*, respectively (Table 1). During both experiments, concentrations increased steadily until day 6 and remained relatively stable thereafter (Fig. 1e, f). POC concentrations during *Varied P* were up to 73 µmol L^{-1} (17.65N/1.10P), but not related to the initial PO_4^{3-} addition. In contrast, build-up of POC was more pronounced during *Varied N* with values up to 102±18 µmol L^{-1} determined in treatments with the highest initial NO_3^- supply (20.0N/0.75P) and indicated a clear correlation to the initial NO_3^- treatment (Table 2).

Along with plankton growth, inorganic nutrient concentrations declined (Fig. 2). During *Varied P*, PO_4^{3-} was exhausted on day 5 in the treatments with the lowest initial PO_4^{3-} supply and the highest initial $[NO_3^-]$: $[PO_4^{3-}]$ ratio of 74, i.e. 12.0N/0.25P. In all other treatments, PO_4^{3-} depletion was reached later during the experiment, except for the highest PO_4^{3-} treatment (12.0N/1.75P), in which PO_4^{3-} remained >0.3 µmol L^{-1} until the last experimental day. During the

same experiment, NO_3^- concentrations fell below the detection limit of 0.03 µmol L^{-1} in some of the mesocosms after day 5, but were not depleted in 12.0N/0.25P. During *Varied N*, NO_3^- was exhausted on day 5 in the low N supply mesocosms (2.00N/0.75P and 4.00N/0.75P). On day 6, NO_3^- was still available in treatments with an initial nitrate supply > 12 µmol L^{-1}, and on day 8 NO_3^- was only available in 17.65N/0.40P, the mesocosms with the highest $[NO_3^-]$: $[PO_4^{3-}]$~~NO_3^- : PO_4^{3-}~~ ratio of 84. After the bloom, PO_4^{3-} was below the detection limit in 9 out of 16 mesocosms having $[NO_3^-]$:$[PO_4^{3-}]$ ratios >10.

3.2 Dissolved organic carbon (DOC) and nitrogen (DON)

Averaged for all mesocosms, initial (day 1) DOC concentration was very similar for *Varied P* (95±5 µmol C L^{-1}) and *Varied N* (96±4 µmol C L^{-1}) (Table 1). Throughout both experiments, DOC concentrations increased steadily after day 2, except for day 5, when a slight decrease was observed in most mesocosms (Fig. 3a, b). For *Varied P*, accumulation of DOC with respect to initial concentration (day 1) (ΔDOC) was observed, ranging from 18.8±6.7 µmol L^{-1} (12.0N/0.25P) to 44.0±12.0 µmol L^{-1} (12.0N/0.75P). During *Varied N*, ΔDOC increased also in the course of the experiment with highest values observed at the end of the experiment, ranging from 12.1±1.1 µmol L^{-1} DOC in the treatment with the lowest nitrate supply (2.0N/0.75P) to 74.4±16.6 µmol L^{-1} in 12.0N/0.75P 75, the same treatment that yielded highest ΔDOC during *Varied P*. MD of DOC were not significantly correlated to the initial PO_4^{3-} supply during *Varied P* , but to the initial NO_3^- supply during *Varied N* (p<0.005), indicating a general dependence of DOC accumulation on NO_3^- stocks (Table 2).

On day 1, DON concentration (day 1) was 8.8 ± 1.1 and 11 ± 1.5 µmol L^{-1} for mesocosms of *Varied P* and *Varied N,* respectively. In both experiments, DON concentration decreased after nutrient addition (Fig. 3c, d). During *Varied P*, ΔDON was negative in some of the mesocosms

373 until the Chl *a* maximum on day 5. Values increased slowly between days 6 and 7 before a clear
374 increase was determined for all mesocosms on day 8 with ΔDON accumulation ranging between
375 1.9 and 5.9 µmol L^{-1} (Fig. 3c). During *Varied N*, a clear accumulation of DON was not observed,
376 yielding values of ΔDON of -6.0 to 4.8 µmol L^{-1} at the end of the experiment. On day 8 of both
377 experiments, highest and lowest ΔDON was determined in the treatments with the highest and
378 lowest initial NO_3^- supply at identical PO_4^{3-} supply, respectively. A significant correlation
379 between the initial PO_4^{3-} or NO_3^- supply and DON accumulation, however, was not determined
380 (Table 2).
381 Both, increasing DOC and decreasing DON concentrations resulted in a rise of molar
382 [DOC]:[DON] ratios until the bloom peak during both experiments (data not shown). During
383 *Varied P* [DOC]:[DON] ratios were initially 10.1±0.92, averaged for all mesocosms and ranged
384 between 7.7 and 31 throughout the experiment, with highest values being observed just before the
385 bloom peak. During *Varied N*, [DOC]:[DON] ratios started at 9.1±1.1 and ranged between 6.8
386 and 34 throughout the experiment, with highest values also observed shortly before the bloom
387 peak on day 6.
388
389
390 **3.3 Gel particle abundance**
391 Averaged for all mesocosms, initial (day 1) TEP numerical abundance was 0.97 ± 0.64 x 10^7 L^{-1}
392 for *Varied P* and steadily increased to highest values between 5.9 x 10^7 and 1.5 x 10^8 L^{-1} until
393 the end of the study (Fig. 4a). TEP total area behaved similar to TEP numerical abundance;
394 values increased from an initial 4.46 ± 2.36 x 10^7 µm² L^{-1} to values between 3.9 x 10^8 and 7.9x
395 10^8 µm² L^{-1} on day 8 (data not shown). Variation of initial NO_3^- concentrations during *Varied N*
396 induced clearly stronger responses in TEP formation than variation of initial PO_4^{3-} concentration

(Fig. 4b). From an averaged $1.07 \pm 0.34 \times 10^7$ L^{-1}, TEP abundance increased until day 8 to values of $1.1 \times 10^8 - 2.8 \times 10^8$ L^{-1}. While initial numbers were in a comparable range for both experiments, the maximum TEP abundances (day 8) during *Varied N* were about twice as high as during *Varied P*. The same holds for TEP total area: Initial averaged values were only slightly higher ($5.04 \pm 1.43 \times 10^7$ µm² L^{-1}) than initial values during *Varied P*, but highest values more than doubled on day 8 during *Varied N*, yielding 9.6×10^8 -1.6×10^9 µm² L^{-1} (data not shown).

During both experiments, TEP numbers and total area increased similarly in all treatments until the Chl *a* maximum. From day 6 onwards, however, distinct differences emerged between treatments, particularly during *Varied N*. Here, TEP abundance was significantly higher in the highest NO_3^- treatment (20.0N/0.75P) compared to treatments amended with lower nitrate supply (2.0N/0.75P; $p<0.001$, 4.0N/0.75P; $p<0.005$, 6.0N/1.03P; $p<0.05$). On day 7, TEP numbers in 20.0N/0.75P reached their maximum and were significantly higher than in all other treatments ($p<0.001$), where TEP numbers continued to increase on day 8. Like TEP numbers, TEP total area was also significantly larger in the highest NO_3^- treatment (20.0N/0.75P) compared to 2.0N/0.75P and 6.0N/1.03P ($p<0.01$) showing a clear stimulation of TEP formation at higher nitrate levels.

For *Varied P*, initial PO_4^{3-} concentration had on average no significant effect on MD of TEP abundance (Table 2). In contrast, a significant positive relationship between MD of TEP abundance and initial NO_3^- supply was determined during *Varied N* ($p<0.001$). This relationship, however, reversed when MD of Chl a normalized TEP concentration were considered, indicating that a relatively higher fraction of newly fixed organic carbon was partitioned into TEP at lower nitrate supply on a cellular level ($p<0.001$; data not shown).

Similar to TEP, CSP abundance and total area increased steadily over time during both mesocosm experiments, albeit CSP were generally less abundant than TEP (Fig. 4c, d). From an initial mean value of 1.06 ± 0.61 x 10^6 L^{-1} during *Varied P,* CSP numerical abundance increased to 4.2 x 10^6 to 1.0 x 10^7 L^{-1} on day 8. Highest CSP abundance was determined in the treatment with the highest nitrate supply (17.65N/1.10P), where CSP total area of initially 1.5 ± 0.5 x 10^7 µm² L^{-1} increased to 4.5 x 10^7 - 1.2 x 10^8 µm² L^{-1} on day 8. Similar to TEP, a much stronger increase in CSP abundance was observed during *Varied N*. Here, CSP numbers increased from an initial average of 1.63 ± 0.48 x 10^6 L^{-1}, to highest values of 1.4 x 10^7 - 2.8x 10^8 L^{-1} on day 7 (Fig. 5d); more than double the amount observed during *Varied P*. Again, highest CSP abundances were determined in replicate treatments of highest NO_3^- supply (20.0N/0.75P) yielding 2.7±0.1 x 10^7 L^{-1}.

Analysis of variance for data obtained on day 7 revealed significantly higher CSP abundances in 20.0N/0.75P compared to 2.0N/0.75P (p<0.001), 4.0N/0.75P (p<0.001) and 6.35N/0.40P (p<0.05), indicating a stimulation of CSP formation at elevated initial NO_3^- concentrations. This is in accordance with a highly significant correlation of MD of CSP abundance and initial NO_3^- concentrations (p< 0.001, Table 2). Findings for CSP numbers are reflected in CSP total area: highest values were also observed for the high NO_3^- treatment (20.0N/0.75P; 213±21 x 10^6 µm² L^{-1}) with values significantly larger than in 2.0N/0.75P (p<0.005), 4.0N/0.75P (p<0.001), 6.35N/0.40P (p<0.001), 17.65N/1.10P (p<0.05) and 12.0N/0.75P (p<0.005) (data not shown). In contrast to TEP abundance, CSP number declined in most treatments on day 8 of *Varied N* (except for 12.0N/0.75P; only MK 1, 6.35N/0.40P and 4.0N/0.75P; only MK 11).

3.4. Gel particle size distributions

445 At the beginning of the study, median values for TEP equivalent spherical diameter (ESD) were
446 almost identical for *Varied P* and *Varied N,* yielding 1.78 ± 0.12 and 1.79 ± 0.08 µm ESD,
447 respectively. Except for days 6 and 8, median size of TEP was steadily increasing over time in
448 *Varied P*, with largest particles occurring in 6.35N/1.10P, 12.0N/1.75P and 12.0N/1.25P on day 7
449 (2.28 - 2.30 µm ESD). On day 8, median TEP size was slightly smaller again and similar in all
450 treatments ranging between 1.80 and 2.26 µm ESD. During *Varied N*, size of TEP remained
451 relatively constant between days 1-4 and then increased until the Chl *a* maximum. After the
452 bloom peak, median TEP size further increased until day 6 yielding values between 2.5 and 1.9
453 µm ESD at the end of the experiment.
454 Spectral slopes describe the size frequency distribution of particles with more negative values
455 indicating relatively more small particles (Fig. 5) and mirrored changes in the median ESD of
456 both types of gel particles during both experiments. Changes in size frequency distribution of
457 TEP were observed for *Varied P* and *Varied N*, with slope values (δ) becoming significantly
458 smaller during the first half of both experiments ($p<0.001$; multiple comparison, Holm-Sidak)
459 (Fig. 6). Average slopes on day 1 were very similar for *Varied P* and *Varied N*, yielding δ=-1.81
460 ± 0.12 and δ=-1.81 ± 0.11, respectively. Slopes increased to average -1.44±0.06 (*Varied P*) and -
461 1.38 ± 0.06 (*Varied N*) on day 8 of both experiments suggesting a relative shift from smaller to
462 larger TEP (Fig. 6a, b).
463
464 Slightly smaller than TEP, median CSP size was on average 1.37 ± 0.06 µm ESD at the
465 beginning of *Varied P*, and increased to values between 1.13 and 1.78 µm ESD until the end of
466 the experiment (Fig. 6cb, ~~left~~). During *Varied N,* median CSP size increased between day 1 (1.36
467 ± 0.09 µm ESD) and day 4 (1.34-1.85 µm ESD). In contrast to median TEP size, median CSP
468 decreased towards the end of the experiments and ranged between 1.18 and 1.71 µm ESD on day

8. During *Varied P*, a large variability of δ values was observed for CSP size distribution on day 1. To estimate changes in size distribution during this experiment, data evaluation of CSP slopes was started on day 2 (Fig. 6c), when CSP size distribution was more similar between mesocosms. Like for TEP, development of CSP spectral slopes during this study mirrored the change in median ESD size of particles. Averaged for all mesocosms, δ=-1.40 ± 0.14 was obtained on day 2 of *Varied P* increasing steadily to -1.24 ± 0.23 until day 8. The size frequency distribution of CSP during *Varied P* was not affected by the initial nutrient supply. For *Varied N*, initial slopes also scattered on day 1, however not as strong as for initial values for *Varied P*. Initial averaged slopes for all mesocosms were -1.64 ± 0.28 (Fig. 6d). During days 2-4, the overall development shows a relative increase in the slope of the size distribution during the onset of the bloom. Highest values of δ=-0.84 coincided with the largest median ESD of CSP on day 4. At the time of the Chl *a* maximum, slopes became more negative, revealing higher abundance of relatively small particles. Multiple comparison (Holm-Sidak) tests revealed significantly larger slopes for days 2 to 4, compared to days 1, 6, 7 and 8 (p<0.010). The increase in abundance of smaller CSP continued during the bloom decay and was most pronounced in 2.0N/0.75P and 4.0N/0.75P, the treatments with the lowest initial NO_3^- supply.

3.5. Differences between two mesocosms experiments - a case of treatment effects?

Although the development of gel particle abundance was rather similar for TEP and CSP during both experiments, particularly until the bloom peak, abundance of gel particles was clearly higher during the second mesocosm experiment, *Varied N,* compared to *Varied P* (Fig. 4). Moreover, during *Varied N,* CSP increased relatively more than TEP and showed a unique change of size distributions during bloom development not observed during *Varied P* and different from TEP.

In order to identify differences between the two series of mesocosms~~s~~ experiments, gel particle abundance was ~~related~~ compared to bloom development, which also differed between the experiments.

During both experiments, gel particle dynamics were tightly coupled to the production of organic matter during bloom development (Fig. 7, Table 3). Numerical abundances of TEP and CSP were directly related to Chl *a* concentration until the bloom peak (Fig. 7a, d). Thereby, the increase of gel particle~~s~~ abundance with Chl *a* concentration was different for TEP and CSP during *Varied P* as well as during *N*. While TEP abundance increased slightly faster with Chl *a* concentration during *Varied P*, the increase in CSP abundance with Chl *a* concentration was twice as strong during *Varied N* than during *Varied P* (Table 3). After the Chl *a* maxima, gel particle formation continued while Chl *a* concentrations declined, leading to higher [gel particles]:[Chl *a*] ratios towards the end of the experiments (Table 4). Partly decoupled from Chl *a* concentration, gel particles remained tightly coupled to POC and PN dynamics throughout both experiments (Fig. ~~8b f~~7b, c, e, f). Thereby, a similar coupling was observed between TEP and POC or PN concentration during both experiments, while CSP abundance increased more strongly with POC and PN concentration during *Varied N* (Table 3). The carbon content of TEP (TEP-C) averaged for all mesocosms on day 1 was 0.61 ± 0.29 µmol L^{-1} and 0.72 ± 0.38 µmol L^{-1} for *Varied P* and *Varied N*, respectively. During both experiments, TEP-C steadily increased along with the general abundance of TEP. Maximum TEP-C during *Varied P* was reached on day 8 with values of 12.6 – 34.9 µmol L^{-1} representing a share of 31-41 Mol% POC, or 8.4-17.6 Mol% TOC (Table 4). During *Varied N*, final TEP-C concentration contributed with an even higher proportion to organic carbon pool, equivalent to 22.8-84 Mol % POC or 12-29 Mol % of TOC. Molar ratios of [TEP-C]:[PN] ~~(mol:mol)~~ were initially below 1 and increased to averaged 2.2-3.6 during *Varied P* and to 1.8-6.9 during *Varied N*.

A direct coupling was also observed between gel particles and bacterial abundance (Table 3). Like for POC and PN, the relative increase in gel abundance was much steeper during *Varied N* than during *Varied P*, again showing that gel particles in general were more abundant during the second experiment. Although less pronounced than for particulate organic matter, TEP and CSP numerical abundances were also related to DOC concentration during *Varied P* and *Varied N* (Table 3), while no significant relationship was observed between gel particle abundance and DON concentration. In contrast to gel particles, however, DOC was not significantly related to Chl *a* concentration in both experiments, but to POC and PN concentrations (Fig. 7g-i, Table 3). Differences in the relationship of DOC to POC or PN were relatively small, suggesting an only slightly higher increase of DOC with particulates during *Varied N*. DOC concentration correlated significantly with bacterial abundance (Table 3). The~~reby~~ increase of DOC concentration relative to bacterial numbers was almost twice as high during *Varied N*, suggesting that bacteria didn't catch up with DOC production during the second experiment.

Another comparison of both experiments can be made by relating gel particle abundance to initial [DIN]:[DIP] ratios that covered a similar range during both experiments (Fig. 8). This showed that for similar initial nutrient ratios, maximum abundance of both TEP and CSP were generally higher during the second experiment, *Varied N*. Moreover, only during the second experiment changes in [DIN]:[DIP] ratios had an effect on maximum gel particle abundance.

However, direct comparison of the 'centre-point' treatment 12.0N/0.75P that was realized with 4 replicates during *Varied P* and 3 replicated during *Varied N* showed clear differences in organic matter development during the two experiments for mesocosms that received the same nutrient addition (Fig. 9). For this treatment, Chl a concentration, DOC and TEP accumulated about two times more in the course of *Varied N*, while the increase in CSP abundance over time was even

Formatiert: Schriftart: Kursiv

threefold higher. ~~This suggests that factors in addition to the nutrient treatments were responsible for the different outcomes of the experiments.~~

4. Discussion

4.1 Nutrient availability and phytoplankton bloom development

After fertilization with inorganic nutrients, phytoplankton blooms developed in all mesocosms during the two consecutive experiments conducted with natural surface water from the eastern tropical North Atlantic (ETNA). Responses to varied nutrient supply became more obvious after one (or both) macronutrients were exhausted, resulting in a large variation of organic matter concentration among mesocosms and treatments during the bloom peak and post-bloom phases. Accumulation of organic matter during bloom development revealed a generally stronger fertilization effect after addition of different amounts of NO_3^- in the second experiment compared to the first one with varied initial PO_4^{3-} supply. This indicates that biomass production in ETNA surface waters near Cape Verde may be limited by nitrogen rather than by phosphorus availability. However, clear differences between both experiments were also observed for mesocosms receiving the same nutrient supply. This suggests that small differences in the initial conditions of experiments with natural communities, such as during this mesocosm~~s~~ study, can significantly impact the outcome of biogeochemical responses.

Moderate variations in responses of planktonic food webs and associated biogeochemical cycling to the same nutrient treatment have been observed previously for mesocosm~~s~~ experiments conducted at different marine ecosystem sites, but a coherent picture of nitrogen stimulation was clearly demonstrated (Olsen et al., 2006; Vadstein et al., 2012).

During this study, phytoplankton abundance was lower during the early days of *Varied N*, while bacterial abundance was higher, despite sampling of initial waters at the same location and within a time difference of only a few days~~,~~. Moreover, differences between *Varied N* and *P* were identified for the initial community composition of diazotrophs (Meyer et al., ~~*in prep.*~~ 2015). We cannot fully exclude that these differences in the initial conditions generally affected the sensitivity to nutrient addition, regardless of the varied nutrient and were also responsible for the higher response in mesocosms where the same nutrient treatment was applied. However, the clear increase in organic matter accumulation with increasing initial NO_3^- concentration is in accordance with~~together with~~ previous findings (Franz et al., 2012a) and strongly suggests that ecosystems in the ETNA are controlled by NO_3^- rather than by PO_4^{3-} availability.

Formatiert: Schriftart: Nicht Kursiv

It should be kept in mind that mesocosm experiments such as conducted during this study can only capture a transient response to perturbation, such as nutrient addition, and mainly give insights to short-term effects on processes. To extrapolate from mesocosm experiments to long~~er~~-term~~ed~~ responses of natural systems is not straightforward. Hence, although the response to NO_3^- addition during the second experiment was pronounced, it represents only one possible outcome. The observed differences for the 12.0N/0.75P treatment indicate that the response of an ecosystem to ~~a potential variability of ecological responses towards~~ nutrient supply may vary even in a comparatively stable environment like the ETNA. Clearly, a better knowledge of the impact of ecological variability, e.g. plankton community structure, diversity and acclimation potential, on biogeochemical processes is needed to fully explain differences in the response size to perturbation.

4.2 Nutrient effects on gel particle~~s~~ dynamics

Previous studies on TEP and CSP in marine systems have suggested that the rate of gel-particle formation depends on the amount and chemical quality of dissolved precursors (Engel et al., 2004aa; Mari and Robert, 2008; Szlosek Chow et al., 2015). For extracellular organic matter released by bacterio- and phytoplankton, the chemical composition and molecular weight of compounds varies among species, and is also dependent on environmental conditions and physiological status (Aluwihare and Repeta, 1999; Grossart et al., 2007; Borchard and Engel, 2015). Because extracellular release is a major source for gel particle precursors, factors influencing this extracellular release likely also affect marine gel particle formation.

During this study, a clear accumulation of DOC was observed along with biomass build-up in all mesocosms, indicating that the rate of DOC release exceeded DOC loss processes such as coagulation into gel- particles or microbial uptake and respiration. Higher ΔDOC values were observed shortly after the Chl *a* peak, coinciding with nutrient concentrations being strongly reduced. Enhanced extracellular release of DOC or 'malfunctioning' of the microbial loop, i.e. reduced microbial uptake and respiration of DOC by bacteria, have been suggested to explain DOC accumulation in the ocean, particularly at times when inorganic nutrients become depleted (Myklestad, 1974; Biddanda and Benner, 1997; Thingstad et al., 1997; Engel et al., 2004b). During this study, DOC accumulation was significantly related to the initial NO_3^- concentration during *Varied N*, suggesting a dependence on the trophic status, although no direct relationship to Chl *a* concentration was observed. Higher accumulation of DOC with increasing nitrogen load has been observed during previous mesocosm experiments and explained by a combination of production and recycling of DOC being both higher at higher microbial biomass (Vadstein et al., 2012). In addition, phosphorus limitation may have reduced bacterial utilisation of DOC in mesocosms with high initial [DIN]:[DIP] ratios and below detection levels of PO_4^{3-} after the bloom, when highest accumulation rates of DOC occurred.

609 In contrast to DOC, no accumulation of DON was observed in the course of the experiments in
610 almost all mesocosms, except for the last day of *Varied P* and for those treatments receiving
611 highest NO_3^- additions during *Varied N*. This indicates that loss processes such as microbial
612 utilization of organic nitrogen forms or partitioning of DON into CSP exceeded DON release
613 during this study.

614 In general, little is known about gel particle~~s~~ production at tropical open ocean sites. To the best
615 of our knowledge, this is the first report on TEP and CSP abundance in the ETNA. Data on TEP-
616 C concentration observed during our study (Table 4), however, agree well with observations from
617 Wurl et al. (2011), who determined <2 to 40 µmol C L^{-1} for TEP in surface waters of the Tropical
618 North Pacific~~,~~(offshore Hawaii).

619 Like DOC, gel-particle~~s~~ abundance during this study was strongly related to the general build-up
620 and decay of autotrophic biomass. Thereby, a significant impact of initial NO_3^- supply on gel
621 particle~~s~~ abundance, especially on CSP, was observed during *Varied N*, as well as a general
622 increase of the maximum abundance of gel particles with the initial [DIN]:[DIP] ratio.

623 An increase of TEP formation, when phytoplankton was grown at higher NO_3^- concentration, is
624 in accordance with earlier observations made during culture and mesocosm~~s~~ experiments (Corzo
625 et al., 2000; Pedrotti et al., 2010) and has been explained by higher biomass production at higher
626 nutrient loads; a larger biomass leads to a higher amount of released polysaccharides when the
627 autotrophic biomass runs into nutrient limitation. A general relationship between TEP and
628 autotrophic biomass concentration, e.g. determined as Chl *a,* has been observed before (Passow,
629 2002; Beauvais et al., 2003). Furthermore, species or physiology specific variations in TEP
630 formation by phytoplankton were observed (Berman and Viner-Mozzini, 2001; Claquin et al.,
631 2008; Passow, 2002~~; Underwood et al., 2004~~). During this study, gel particles and Chl *a*

dynamics were decoupled after the Chl *a* peak. Hence, despite the general observation that higher autotrophic biomass leads to more gel particles, temporal developments of Chl *a* and gel particle concentration may contrasts between bloom built-up and decay. This is in accordance with earlier studies showing that POC, TEP and CSP concentration continued to increase after the Chl *a* peak (Alldrege, 1995; Engel, 2002; Logan et al., 199~~5~~4; Mari and Kiørboe, 1996) and can be explained by the 'carbon-overflow' theory (Schartau et al., 2007; Kreus et al., 2015).

During the post-bloom phase, a large proportion of organic carbon was thus channeled to the POC pool in the form of TEP. Carbon contained in TEP, accounted for 0.5 µmol C (initial days) to ~68 µmol C (final days) indicating a much higher DOC production than derived from ΔDOC alone. The ratio of [TEP-C]:[POC] strongly increased during *Varied N,* yielding values of up to 93%. Even though these values are within the range of earlier findings (Engel and Passow, 2001; Pedrotti, 2010), an underestimation of POC, and hence overestimation of [TEP-C]:[POC] ratio, seems likely, because a large proportion of TEP was in the size range 1-2 µm ESD and may not be retained on GF/F filters (nominal pore size 0.7 µm), due to their flexible and non-spherical structure (Engel and Passow, 2001; Pedrotti, 2010). In addition, TEP-C calculation by use of an empirical relationship to TEP size previously established from phytoplankton cultures could overestimate carbon content of naturally occurring TEP at this site.

A recent study by Rahav et al. (2013) suggested that bacterial diazotrophs in aphotic, DIN-rich layers of the Red Sea and eastern Mediterranean Sea benefit from TEP as organic carbon source, resulting in an increase in aphotic nitrogen fixation with TEP concentration. For the ETNA, unicellular heterotrophic diazotrophs are readily abundant, also below the euphotic zone in high DIN waters (Langlois et al., 2005), and contribute substantially to total nitrogen fixation of the system (Agawin et al., 2014). High TEP production by surface phytoplankton communities in the

655 ETNA as observed during this study, and settling of TEP to aphotic layers, may therefore provide
656 an important labile carbon source for sustaining heterotrophic nitrogen fixation.

657 While the importance of TEP formation for converting DOC to POC, and related consequences
658 for carbon cycling and export, have been highlighted over the past decades (Alldrege et al., 1995;
659 Passow, 2002; Engel et al., 2004a; Arrigo, ~~2005~~2007), little is known ~~on~~ about the role of CSP,
660 on organic carbon and more importantly on organic nitrogen cycling. It is likely that CSP plays a
661 significant role for nitrogen cycling, contributing to DON to PN conversion and to the PN pool as
662 well as providing a nitrogenous resource for auto- and heterotrophic growth.

663 During this study, clearly higher accumulation of CSP relative to Chl *a* was observed during
664 *Varied N*, i.e. when a surplus of inorganic nitrogen was available. As a consequence, CSP
665 contributed more to POC and PON increase during *Varied N* than during *Varied P*. This suggests
666 that higher inorganic nitrogen supply favors production of extracellular PON, which may be
667 subject to bacterial utilization at a later time. Because CSP are proteinaceous particles, their
668 export to depth, e.g. by physical transport or as part of sinking aggregates, may provide important
669 amino acids for microorganisms in aphotic zones, including denitrifying and anammox bacteria.
670 Since labile amino acids have been suggested to be one important factor limiting organic matter
671 degradation in oxygen minimum zones (Pantoja et al., 2004; 2009), a supply with CSP from the
672 photic zone may also affect total carbon remineralisation and therewith oxygen consumption at
673 deeper depths. Our results furthermore suggest that CSP as proteinaceous particles may include
674 an important fraction of organic nitrogen in the size fraction typically attributed to bacteria.

675

676

4.3 Formation, aggregation and degradation of gel particles – Insights from size frequency distributions

Changes in the size frequency distribution of TEP during this study revealed an increase in the proportion of larger particles in the course of phytoplankton blooms, indicating TEP aggregation rather than degradation during both experiments. For CSP, decreasing slopes together with a strong increase in total abundance revealed an increasing number of smaller particles during *Varied N*, indicating new formation of CSP during the phytoplankton bloom ~~peak~~ and ~~until the end of the experiment~~postbloom periods. Occurrence of CSP at the time or depth of the Chl *a* maxima has also been observed during previous studies (Cisternas Novoa et al., 2014; 2015). A clear indication for aggregation processes, i.e. decreasing slopes as for TEP, was not observed for CSP. This is in accordance with findings of Prieto et al. (2002), who suggested that CSP are less involved in aggregate formation during diatom blooms than TEP. ~~Moreover,~~ CSP number and total area decreased at the end of *Varied N* (day 8), suggesting that loss processes exceeded new CSP formation.

Formatiert: Schriftart: Nicht Kursiv

TEP and CSP, both represent hotspots for microbial activity (Azam, 1983; Passow and Alldrege, 1994; Pedrotti, 2009; Grossart, 1998; Bar-Zeev, 2009). However, CSP are per definition proteinaceous particles and thus expected to include high amounts of labile N-compounds. The observed decrease in CSP abundance at day 8 of *Varied N* can therefore be explained by bacterial degradation in order to liberate N, as suggested earlier (Long and Azam, 1998). Bacteria cell numbers sharply increased from day 5 onwards during both experiments, along with the strongest increase in gel-particle abundance.

5. Conclusion

Gel particles can represent a substantial fraction of organic particles in ETNA ecosystems after nutrient supply, e.g. deep upwelling of water masses. Increasing NO_3^- relative to PO_4^{3-} concentrations favors gel particles formation. Consequently, it may be expected that a reduction of NO_3^- surface water concentrations as a result of increasing ocean anoxia will diminish the abundance of marine gel particles, particularly CSP, with potential implications for aggregation, export and turn-over processes of organic matter in the water column. Thereby, particle dynamics of TEP and CSP differ during bloom development; while TEP seem to be more prone to aggregation, potentially enhancing export of organic matter, CSP appear to be a better organic substrate for heterotrophs and may decompose within a few days. Because TEP and CSP are part of the bulk POC and PN pools, changes in the balance of TEP and CSP formation processes such as induced by changes in the $[NO_3^-]$: $[PO_4^{3-}]$ supply ratio will likely impact biogeochemistry during and after phytoplankton blooms as well as food-web dynamics. Biogeochemical responses to variations in nutrient supply and stoichiometry may differ between different pelagic communities, even in supposedly stable ecosystems such as the ETNA.

Acknowledgements

This research was supported by the *Sonderforschungsbereich 754* "Climate-Biogeochemistry Interactions in the Tropical Ocean" (www.sfb754.de), subprojects B2 (J. Meyer), B8 (H. Hauss and R. Kiko) and B9 (A. Engel, C. Borchard, A. Loginova). The *Sonderforschungsbereich 754* is supported by the German Science Foundation (DFG). The authors thank their colleagues from the INDP, Cape Verde, for their assistance with setting up the experiment and acknowledge the support of captain and crew of RV *Islandia* during initial sampling. We furthermore greatly acknowledge the technical support of Jon Roa (DOC, DON) and Ulrike Panknin (nutrients), as well as Nienke Bijma, Clarissa Karthäuser and Sami Manandhar (gel particles microscopy).

References

Agawin, N. S. R., Benavides, M., Busquets, A., Ferriol, P., Stal, L.J., and Aristegui, J.: Dominance of unicellular cyanobacteria in the diazotrophic community in the Atlantic Ocean. Limn. Oceanogr., 59, -2, -623-63, 2014.

Alldredge, A. L., Gotschalk, C., Passow, U., and Riebesell, U.: Mass aggregration of Diatom blooms - Insights from a mesocosm study, Deep-Sea Research Part II-Topical Studies in Oceanography, 42, 9-27, 1995.

Alldredge, A. L., Passow, U., and Logan, B. E.: The abundance and significance of a class of large, transparent organic particles in the ocean, Deep-Sea Res., 40, 1131-1140, 1993.

Aluwihare, L.I., Repeta, D.J.: A comparison of the chemical characteristics of oceanic DOMand extracellular DOM produced by marine algae, Mar. Ecol.- Prog. Ser., 186, 105-117, 1999.

Arrigo, K. R.: Carbon cycle. Marine manipulations. Nature, 450, 491-492, 2007.

Azam, F., Fenchel, T., Field, J.G., Graf, J. S., Meyer-Rei, L. A., and Thingstad, F.: The ecological role of water- column microbes in the sea. Mar. Ecol. Prog. Ser., 10, 257-263, 1983.

~~Azam, F., Long, R, A.: Oceanography - Sea snow microcosms, Nature, 414, 495, 2001.~~

Baines, S. B. and Pace, M. L.: The production of dissolved organic matter by phytoplankton and its importance to bacteria: Patterns across marine and freshwater systems, Limnol. Oceanogr., 36, 1078-1090, 1991.

Feldfunktion geändert
Feldfunktion geändert
Feldfunktion geändert
Feldfunktion geändert
Feldfunktion geändert

Formatiert: Schriftart: Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Englisch (USA)
Formatiert: Englisch (USA)

Baker, A.R., Weston, K., Kelly, S.D., Voss, M., Streu, P., Cape, J. N.: Dry and wet deposition of nutrients from the tropical Atlantic atmosphere: links to primary productivity and nitrogen fixation. Deep-Sea Res., I 54, 10, 1704–1720, 2007.

Bar-Zeev, E., Berman-Frank, I., Stambler, N., Vázquez-Domínguez, E., Zohary, T., Capuzzo, E., Meeder, E., Suggett, D.J., Iluz, D., Dishon, G., and Berman, T.: Transparent exopolymer particles (TEP) link phytoplankton and bacterial production in the Gulf of Aqaba, Aquat. Microb Ecol, 56, 217-225, doi: 10.3354/ame01322, 2009.

Beauvais, S., Pedrotti, M. L., Villa, E., and Lemee, R.: Transparent exopolymer particle (TEP) dynamics in relation to trophic and hydrological conditions in the NW Mediterranean Sea, Mar. Ecol. Prog. Ser., 262, 97-109, 2003.

Berman, T., and Viner-Mozzini, Y.: Abundance and characteristics of polysaccharide and proteinaceous particles in Lake Kinneret, Aquat. Micr. Ecol., 24, 255-264, 2001.

Biddanda, B., and Benner, R.: Carbon, nitrogen, and carbohydrate fluxes during the production of particulate and dissolved organic matter by marine phytoplankton, Limnol. Oceanogr., 42, 506-518, 1997.

Bjørnsen, P.K.: Phytoplankton exudation of organic matter: Why do healthy cells do it?, Limnol. Oceanogr., 33, 151-154, 1988.

Borchard,C., Borges, A., Händel, N. and Engel, A. Biogeochemical response of *Emiliania huxleyi* (PML B92/11) to elevated CO_2 and temperature under phosphorous limitation: a chemostat study. Journal of Experimental Marine Biology and Ecology, 410 . pp. 61-71, 2011.

Feldfunktion geändert

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

Feldfunktion geändert

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

Formatiert: Schriftart: Kursiv

Formatiert: Schriftart: Kursiv

Formatiert: Tiefgestellt

Borchard, C., and Engel, A.: Organic matter exudation by *Emiliania huxleyi* under simulated future ocean conditions Biogeosciences (BG), 9 (8). pp. 3405-3423. DOI 10.5194/bg-9-3405-2012, 2012.

Borchard, C. aund Engel, A.: Size-fractionated dissolved primary production and carbohydrate composition of the coccolithophore *Emiliania huxleyi,* Biogeosciences, 12, 1271-1284, 2015.

Chin, W.C., Orellana, M.V., and Verdugo, P.: Spontaneous assembly of marine dissolved organic matter into polymer gels, Nature, 391, 568-572, 1998.

~~Carlson, C.A.: Production and removal processes. Biogeochemistry of Marine Dissolved Organic Matter. In Hansell, D. A. and Carlson, C. (eds) Academic Press, Elsevier Science San Diego, CA, USA, 91-139, 2002.~~

~~Chen, F.: Nutrients, in: Encyclopedia of Tidepools and Rocky Shores, Denny, M.W. and Gaines, S.D. (eds.), University of California Press, 404-408, 2007.~~

Cisternas-Novoa, C., Lee, C., and Engel, A.: A semi-quantitative spectrophotometric, dye-binding assay for determination of Coomassie Blue stainable particles. Limnol. Oceanogr. Methods, 12, 604-616, 2014.

Cisternas-Novoa, C., Lee, C., and Engel, A.: Transparent exopolymer particles (TEP) and Coomassie stainable particles (CSP): Differences between their -origin and vertical distributions in the ocean. Mar. Chem., 175, 56-71, 2015~~ (in press)~~.

Feldfunktion geändert

Feldfunktion geändert

Feldfunktion geändert

Formatiert: Englisch (Großbritannien)

Feldfunktion geändert

Claquin, P., Probert, I., Lefebvre, S., and Veron, B.: Effects of temperature on photosynthetic parameters and TEP production in eight species of marine microalgae. Aquat. Micr. Ecol. 51, 1-11, 2008.

Corzo, A; Morillo, JA; and Rodriguez, S.: Production of transparent exopolymer particles (TEP) in cultures of *Chaetoceros calcitrans* under nitrogen limitation, Aquatic Microb. Ecol., 23, 1, 63-72, 2000.

Del Giorgio, P. A. and Duarte, C.:Respiration in the open ocean. Nature, 420, 379-384, 2002.

Deutsch, C., Sarmiento, J. L., Sigman, D. M., Gruber- , N., and Dunne, J. P.: Spatial coupling of nitrogen inputs and losses in the ocean, Nature, 445, 7124, 163-167, 2007.

Ducklow H.W., Purdie D.A., Williams P.J.L., and Davies J.M.: Bacterioplankton - a sink for carbon in a coastal marine plankton community, Science, 232, 865-867, 1986.

Engel, A., and Passow, U.: Carbon and nitrogen content of transparent exopolymer particles (TEP) in relation to their Alcian Blue adsorption, Mar Ecol-Prog Series, 219, 1-10, 2001.

Engel, A.: Direct relationship between CO2 uptake and transparent exopolymer particles production in natural phytoplankton, J. Plankton Res., 24, 49-53, 2002.

Engel, A., Thoms, S., Riebesell, U., Rochelle-Newall, E. and Zondervan, I.: Polysaccharide aggregation as a potential sink of marine dissolved organic carbon, Nature, 428 , 929-932, 2004aa.

Engel, A., Delille, B., Jacquet, S., Riebesell, U., Rochelle-Newall, E., Terbrüggen, A. and Zondervan, I.: Transparent exopolymer particles and dissolved organic carbon production

Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Feldfunktion geändert
Feldfunktion geändert
Feldfunktion geändert
Feldfunktion geändert
Feldfunktion geändert
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Feldfunktion geändert
Feldfunktion geändert
Feldfunktion geändert

by *Emiliania huxleyi* exposed to different CO_2 concentrations: a mesocosm experiment, Aquat. Microb. Ecol., 34, 93-104, 2004b.

Engel, A.: Determination of Marine Gel Particles, Practical Guidelines for the Analysis of Seawater. CRC Press. 2009.

Engel, A., Händel, N., Wohlers, J., Lunau, M., Grossart, H. P., Sommer, U. uand Riebesell, U.: Effects of sea surface warming on the production and composition of dissolved organic matter during phytoplankton blooms: results from a mesocosm study, Journal of Plankton Research, 33, 3, 357-372, 2011.

Engel, A., Piontek, J., Grossart, H. P., Riebesell, U., Schulz, K. G. and Sperling, M.: Impact of CO2 enrichment on organic matter dynamics during nutrient induced coastal phytoplankton blooms, Journal of Plankton Research, 36, 641-657, 2014.

~~Engel, A., Piontek, J., Grossart, H. P., Riebesell, U., Schulz, K. G. and Sperling, M.: Impact of CO2 enrichment on organic matter dynamics during nutrient induced coastal phytoplankton blooms, Journal of Plankton Research, 36, 641-657, 2014.~~

Falkowski, P.G.: Rationalizing elemental ratios in unicellular algae. J. Phycol., 36: 3-6, 2000.

~~Finkel, Z.V., Beardall, J., Flynn, K.J., Quigg, A., Rees, T.A.V., and Raven J.A.: Phytoplankton in a changing world: cell size and elemental stoichiometry, J. Plank Res, 32, 1, 119-137, 2010.~~

Fogg, G.E.: The ecological significance of extracellular products of phytoplankton photosynthesis, Bot. Mar., 26, 3-14, 1983.

Feldfunktion geändert

Feldfunktion geändert

Feldfunktion geändert

Fraga, F. Phytoplanktonic biomass synthesis: application to deviations from Redfield stoichiometry, Sci. Mar., 65, 153-169, 2001.

Franz, J. M. S., Hauss, H., Sommer, U., Dittmar, T., and Riebesell, U: Production, partitioning and stoichiometry of organic matter under variable nutrient supply during mesocosm experiments in the tropical Pacific and Atlantic Ocean. Biogeosciences, 9, 4629-4643, doi:10.5194/bg-9-4629-2012, 2012a.

Franz, J., Krahmann, G., Lavik, G., Grasse, P., Dittmar, T., and Riebesell, U.: Dynamics and stoichiometry of nutrients and phytoplankton in waters influenced by the oxygen minimum zone in the eastern tropical Pacific, Deep-Sea Res. Part I, 62, 20-31, 2012b.

Galgani, L., Stolle, C., Endres, S., Schulz, K. G. und Engel, A.: Effects of ocean acidification on the biogenic composition of the sea-surface microlayer: Results from a mesocosm study, Journal of Geophysical Research - Oceans, 119, 7911-7924. DOI 10.1002/2014JC010188, 2014

Geider, R. J. and LaRoche, J.: Redfield revisited: variability of C:N:P in marine microalgae and its biochemical basis, Eur. J. Phycol., 37, 1-17, 2002.

Goldman, J.C., McCarthy, J.J., Peavey, D.G.: Growthrate influence on the chemical composition of phytoplankton in oceanic waters, Nature, 279, 210-215, 1979.

Grasshoff K., Kremling K., and Ehrhardt M.: Methods of seawater analysis, 3rd ed. Wiley1999.

~~Graziano, L. M., Geider, R. J., Li, W. K. W., and Olaizola, M.: Nitrogen limitation of North Atlantic phytoplankton: Analysis of physiological condition in nutrient enrichment experiments, Aquat. Microb. Ecol. 11, 53-64, 1996.~~

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

Formatiert: Schriftart: Kursiv

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

Feldfunktion geändert

Formatiert: Englisch (USA)

852 Grossart, H.P., Berman, T., Simon, M., and Pohlmann, K.: Occurrence and microbial dynamics
853 of macroscopic organic aggregates (lake snow) in Lake Kinneret, Israel, in fall, Aquat.
854 Microb. Ecol., 14, 59-67, 1998.

855 Grossart, H., Engel, A., Arnosti, C., De La Rocha, C. L., Murray, A. E., and Passow, U.:
856 Microbial dynamics in autotrophic and heterotrophic seawater mesocosms. III. Organic
857 matter fluxes, -Aquat. Microb. Ecol. , 49, 143-156, 2007.

858 Gruber, N., and Sarmiento, J.L.: Global patterns of marine nitrogen fixation and denitrification,

859 Hansell, D. A., Bates, N. R., and Olson, D. B.: Excess nitrate and nitrogen fixation in the North
860 Atlantic Ocean. Mar. Chem., 84, 3–4, 243–265, 2004.

861 **Hauss, H**., Franz, J.M.S., Hansen, T., Struck, U. and Sommer U. Relative inputs of upwelled and
862 atmospheric nitrogen to the eastern tropical North Atlantic food web: Spatial distribution
863 of $\delta^{15}N$ in meso zooplankton and relation to dissolved nutrient dynamics. Deep-Sea
864 Research I 75: 135–145, 2013, doi: 10.1016/j.dsr.2013.01.010

865 **Hauss, H**., Franz, J.M.S. and Sommer U., Changes in N:P stoichiometry influence taxonomic
866 composition and nutritional quality of phytoplanton in the Peruvian Upwelling. Journal of
867 Sea Research 73: 74-85, 2012, doi: 10.1016/j.seares.2012.06.010

868 Karstensen, J., Fiedler, B., Schütte, F., Brandt, P., Körtzinger, A., Fischer, G., Zantopp, R., Hahn,
869 J., Visbeck, M., and Wallace, D.: Open ocean dead-zone in the tropical North Atlantic
870 Ocean, Biogeosciences Discuss., 11, 17391-17411, doi:10.5194/bgd-11-17391-2014,
871 2014.

Feldfunktion geändert

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

Klausmeier, C.A., Litchman, E., Daufresne, T., and Levin, S. A.: Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton, Nature, 429, 171-174, 2004.

Kreus, M., Schartau, M., Engel, A., Nausch, M., and Voss, M.: Variations in the elemental ratio of organic matter in the central Baltic Sea: Part I—Linking primary production to remineralization, Continental Shelf Research, 100, 25-45, 2015. DOI 10.1016/j.csr.2014.06.015 ~~Variations in the elemental ratio of organic matter in the central Baltic Sea: Part I—Linking primary production to remineralization, Continental Shelf Res. DOI 10.1016/j.csr.2014.06.015. 2014.~~

Kuypers, M. M. M., Lavik, G., Woebken, D., Schmid, M., Fuchs, B. M., Amann, R., Jørgensen, B. B., and Jetten, M. S. M.: Massive nitrogen loss from the Benguela upwelling system through anaerobic ammonium oxidation, Proc. Natl. Acad. Sci. 102, 6478–6483, doi: 10.1073/pnas.0502088102, 2005.

Lam, P., and Kuypers, M.M.M: Microbial Nitrogen Cycling Processes in Oxygen Minimum Zones. Annu. Rev. Mar. Sci., 3, 317–45, 2011.

Langlois, R. J., LaRoche, J., and Raab, P. A.: Diazotrophic Diversity and Distribution in the Tropical and Subtropical Atlantic Ocean, Appl. Environ. Microbiol., 71, 7910-7919, 2005.

Logan, B. E., Grossart, H.-P., and Simon, M.: Direct observation of phytoplankton, TEP and aggregates on polycarbonate filters using brightfield microscopy, J. Plankt. Res., 16, 1811-1815, 1994.

Long, R.A., and Azam, F.: Abundant protein-containing particles in the sea, Aquat. Microb. Ecol., 10, 213-221, 1996.

Feldfunktion geändert
Formatiert: Unterstrichen
Formatiert: Schriftart: Nicht Kursiv, Nicht unterstrichen, Englisch (USA)
Feldfunktion geändert
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Feldfunktion geändert
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Feldfunktion geändert
Feldfunktion geändert
Formatiert: Schriftart: Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32)), Englisch (USA)
Formatiert ...

Mague, T.H., Friberg, E., Hughes, D.J., and Morris, I.: Extracellular release of carbon by marine phytoplankton; a physiological approach, Limnol. Oceanogr. 25, 262-279, 1980.

Mari, X., and Kiørboe T.: Abundance, size distribution and bacterial colonization of transparent exopolymeric particles (TEP) during spring in the Kattegat, J. Plankton Res., 18, 969-986, doi: 10.1093/plankt/18.6.969, 1996.

Mari, X., and Robert, M.: Metal induced variations of TEP sticking properties in the southwestern lagoon of New Caledonia. Mar. Chem., 110, 98–108, 2008.

Mari, X.: Carbon content and C:N ratio of transparent exopolymeric particles (TEP) produced by bubbling exudates of diatoms. Mar. Ecol. Progr. Ser., 183, 59-71, 1999.

Meyer, J., Löscher, C. R., Neulinger, S. C., Reichel, A. F., Loginova, A., Borchard, C., Schmitz, R. A., Hauss, H., Kiko, R. and U. Riebesell: Changing nutrient stoichiometry affects phytoplankton production, DOP build up and dinitrogen fixation – a mesocosm experiment in the eastern tropical North Atlantic, Biogeosciences Discuss., 12, 9991-10029, 2015.

~~Mills, M.M., Ridame, C., Davey, M., LaRoche, J., and Geider, R.J., 2004. Iron and phosphorus co-limit nitrogen fixation in the eastern tropical North Atlantic, Nature, 429, 292-294.~~

Mills, M.M., and Arrigo, K.R.: Magnitude of oceanic nitrogen fixation influenced by the nutrient uptake ratio of phytoplankton, Nature Geoscience, 3, 412-416, 2010.

~~Moore, C. M., Mills, M.M., Langlois, R., Milne, A., Achterberg, E.P., LaRoche, J., and Geider, R.J.: Relative influence of nitrogen and phosphorus availability on phytoplankton~~

Formatiert: Englisch (USA)

Formatiert: Schriftart: Nicht Fett, Englisch (USA)

Formatiert: Englisch (USA)

Formatiert: Englisch (USA)

~~physiology and productivity in the oligotrophic sub-tropical North Atlantic Ocean, Limnol. Oceanogr., 53, 291-305, 2008.~~

Myklestad, S.: Production of carbohydrates by marine planktonic diatoms I, Comparison of nine different species in culture, J. exp. mar. Biol. Ecol., 15, 261-274, 1974.

Nagata, T.: Production mechanisms of dissolved matter. In Kirchmann, D. L. (ed.), Microbial Ecology of the Oceans, First edition, Wiley-Liss, New York, 121-152, 2000.

Olsen, Y., Agusti, S., Andersen, T., Duarte, C. M. , Gasol, J. M. , Gismervik, I. , Heiskanen, A-S., Hoell, E., Kuuppo, P. , Lignell, R., Reinertsen, H., Sommer, U., Stibor, H., Tamminen, T., Vadstein, O., Vaque, D., Vidal, M.: A comparative study of responses in planktonic food web structure and function in contrasting European coastal waters exposed to experimental nutrient addition, Limn. Oceanogr., 51, 1, 488-503, 2006.

Pantoja, S., Sepulveda, J. S., and Gonzalez, H. E.: Decomposition of sinking proteinaceous material during fall in the oxygen minimum zone off northern Chile, Deep-Sea Research Part I-Oceanographic Research Papers, 51, 55-70, 10.1016/j.dsr.2003.09.005, 2004.

Pantoja, S., Rossel, P., Castro, R., Cuevas, L. A., Daneri, G., and Cordova, C.: Microbial degradation rates of small peptides and amino acids in the oxygen minimum zone of Chilean coastal waters, Deep-Sea Research Part Ii-Topical Studies in Oceanography, 56, 1019-1026, 10.1016/j.dsr2.2008.09.007, 2009.

Parsons, T.R., Maita, Y., and Lalli, C.M.: A manual of chemical and biological methods for seawater analysis Pergamon Press Oxford, UK, 173pp, 1984.

Feldfunktion geändert

936 Passow, U., Shipe, R.F., Murray, A., Pak, D.K., Brzezinski, M.A., and Alldredge, A.L.: The
937 origin of transparent exopolymer particles (TEP) and their role in the sedimentation of
938 particulate matter. Cont. Shelf Res., 21, 4 , 327-346, 2001.

939 Passow, U.: Transparent exopolymer particles (TEP) in aquatic environments. Prog. Oceanogr.
940 55, 3-4, 287-333, 2002.

941 Pedrotti, M. L., Peters, F., Beauvais, S., Vidal, M., Egge, J., Jacobsen, A., Marrase, C.: Effects of
942 nutrients and turbulence on the production of transparent exopolymer particles: a
943 mesocosm study, Mar. Ecol. Prog. Ser., 419, 57-69, 2010.

944 Prieto, L., Ruiz, J., Echevarría, F., García, C. M., Bartual, A., Gálvez, J. A., Corzo, A., and D.
945 Macías: ~~Prieto, L. et al., 2002.~~ Scales and processes in the aggregation of diatom blooms:
946 high time resolution and wide size range records in a mesocosm study. Deep Sea Res.
947 Part I 49(7), 1233-1253, ~~-~~ 2002.

948 Radic, T., Ivancic, I., Fuks, D., and Radic, J. Marine bacterioplankton production of
949 polysaccharidic and proteinaceous particles under different nutrient regimes. FEMS
950 Microb. Ecol., 58 , 3, 333-342, 2006.

951 Rahav, E., Bar-Zeev, E., Ohayon, S., Elifantz, H., Belkin, N., Herut, B., Mulholland, M. R., and
952 Berman-Frank, I.: Dinitrogen fixation in aphotic oxygenated marine environments.
953 Frontiers in Mar. Microbiol., 4, 227,1-11~~1~~, 2013.

954 Redfield, A. C.: The biological control of chemical factors in the environment. Am. Sci., 46, 205-
955 221, 1958.

Formatiert: Schriftart: (Standard) Times New Roman, 12 Pt., Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Schriftart: (Standard) Times New Roman, 12 Pt., Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Schriftart: (Standard) Times New Roman, 12 Pt., Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Schriftart: (Standard) Times New Roman, 12 Pt., Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Schriftart: (Standard) Times New Roman, 12 Pt., Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Schriftart: (Standard) Times New Roman, 12 Pt., Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Schriftart: (Standard) Times New Roman, 12 Pt., Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Schriftart: (Standard) Times New Roman, 12 Pt., Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Feldfunktion geändert

Feldfunktion geändert

Feldfunktion geändert

Feldfunktion geändert

Redfield, A. C., Ketchum, B. H., and Richards, F. A.: The influence of organisms on the composition of seawater. In: The sea, ideas and observations on progress in the study of the seas, Vol 2, M. N. Hill (editor), Interscience, 26-77, 1963.

Rhee, G. Y.: Effect of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. Limnol. Oceanogr., 23, 10-25, 1978.

Sarmiento, H., and Gruber, N. L.: Global patterns of marine nitrogen fixation and denitrification. Global Biogeochem. Cycles, 11(2), 235-266, 1997~~Ocean Biogeochemical Dynamics. Princeton University Press, 2006.~~

Schartau, M., Engel, A., Schröter, J., Thoms, S., Völker, C., and Wolf-Gladrow, D.: Modelling carbon overconsumption and the formation of extracellular particulate organic carbon, Biogeosciences, 4, 433-454, 2007.

Schneider, B., Engel, A. and Schlitzer, R.: Effects of depth- and CO2-dependent C:N ratios of particulate organic matter (POM) on the marine carbon cycle, Global Biogeochemical Cycles, 18 (2), 1-13. DOI 10.1029/2003GB002184, 2004.

Sharp, J. H.: Improved analysis for particulate organic carbon and nitrogen from seawater Limnol.Oceanogr., 19, 984-989, 1974.

Sharp, J. H.: Excretion of organic matter by marine phytoplankton - Do healthy cells do it? Limnol. Oceanogr., 22, 381-399, 1977.

Formatiert: Schriftart: (Standard) Times New Roman, 12 Pt., Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Feldfunktion geändert

Feldfunktion geändert

Sommer, U; Hansen, T; Stibor, H; and Vadstein, O.: Persistence of phytoplankton responses to different Si : N ratios under mesozooplankton grazing pressure: a mesocosm study with NE Atlantic plankton. Mar. Ecol. Prog. Ser., 278, 67-75, 2004.

~~Sommer, U; Hansen, T; Stibor, H; and Vadstein, O.: Persistence of phytoplankton responses to different Si : N ratios under mesozooplankton grazing pressure: a mesocosm study with NE Atlantic plankton, Mar. Ecol. Prog. Ser., 278, 67-75, 2004.~~

Sterner, R. W., –and Elser, J. J.: Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere ISBN: 9780691074917 464 pp. 2002

Stramma, L., Johnson, G. C., Sprintall, J., and Mohrholz, V.: Expanding Oxygen-Minimum Zones in the Tropical Oceans, Science, 320, 655-658, doi: 10.1126/science.1153847, 2008.

Sugimura, Y., and Suzuki, Y.: A high-temperature catalytic oxidation method for the determination of non-volatile dissolved organic carbon in seawater by direct injection of a liquid sample, Mar. Chem., 24, 2, 105–131, 1988.

Szlosek Chow, J., Lee, C., and Engel, A.: The influence of extracellular polysaccharides, growth rate, and free coccoliths on the coagulation efficiency of *Emiliania huxleyi*. Mar. Chem., ~~submitted.~~175, 5-15, 2015.

Thingstad, T. F., Hagstrom, A., and Rassoulzadegan, F.: Accumulation of degradable DOC in surface waters: Is it caused by a malfunctioning microbial loop?, Limnology and Oceanography, 42, 398-404, 1997.

Feldfunktion geändert

Formatiert: Deutsch (Deutschland)

Formatiert: Deutsch (Deutschland)

Formatiert: Deutsch (Deutschland)

Formatiert: Schriftart: Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Einzug: Links: 0 cm, Hängend: 1,27 cm, Zeilenabstand: Doppelt, Leerraum zwischen asiatischem und westlichem Text nicht anpassen, Leerraum zwischen asiatischem Text und Zahlen nicht anpassen

Formatiert: Schriftart: Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Schriftart: Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Formatiert: Schriftart: Schriftartfarbe: Benutzerdefinierte Farbe(RGB(27;28;32))

Feldfunktion geändert

Feldfunktion geändert

Thornton, D. C. O.: Effect of low pH on carbohydrate production by a 1815 marine planktonic diatom (Chaetoceros muelleri), Research Letters in Ecology, Article ID 105901, 2009.

Toggweiler, J. R.: Carbon overconsumption, Nature, 363, 210-211, 1993.

Vadstein, O., Andersen, T., Reinertsen, H. R., and Olsen, Y.: Carbon, nitrogen and phosphorus resource supply and utilisation for coastal planktonic heterotrophic bacteria in a gradient of nutrient loading. Mar. Ecol. Prog. Ser., 447, 55-75, 2012.

Verdugo, P., Alldredge, A. L., Azam, F., Kirchman, D. L., Passow, U., and Santschi, P. H.: The oceanic gel phase: a bridge in the DOM-POM continuum. Mar. Cem. 92, 67-85, 2004.

Wood, M.A., van Valen, L. M.: Paradox lost? On the release of energy-rich compounds by phytoplankton, Marine Microbial Food Webs 4, 103-116, 1990.

Wurl, O., L. Miller, and Vagle, S. Production and fate of transparent exopolymer particles in the ocean, J. Geophys. Res., 116, C00H13, doi:10.1029/2011JC007342, 2011.

Feldfunktion geändert
Feldfunktion geändert
Feldfunktion geändert
Feldfunktion geändert
Formatiert: Englisch (USA)
Feldfunktion geändert
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Feldfunktion geändert
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Feldfunktion geändert
Feldfunktion geändert
Feldfunktion geändert
Formatiert: Englisch (USA)
Feldfunktion geändert
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)
Formatiert: Englisch (USA)

Tables

Table 1: Summary of initial conditions of the seawater used to fill the mesocosms during the two experiments, target nutrient concentrations (Treat-ID), and different nutrient conditions inside the mesocosms after nutrient addition (day 1).

	Varied P					***Varied N***			
Day 0									
Latitude			16.74°N					16.76°N	
Longitude			25.16°W					25.16°W	
POC [µmol L^{-1}]			13.6 ± 3.8					11.9 ± 1.9	
PON [µmol L^{-1}]			1.85 ± 0.68					1.54 ± 0.26	
POP [µmol L^{-1}]			0.10 ± 0.02					0.07 ± 0.01	
Chl *a* [µg L^{-1}]			0.38 ± 0.09					0.18 ± 0.05	
DOC [µmol L^{-1}]			95 ± 4.6					96± 3.9	
DON [µmol L^{-1}]			8.8 ± 1.1					11 ± 1.5	
Day 1									
Mesocosm	Nitrate [µmol L^{-1}]	Phosphate [µmol L^{-1}]	DIN:DIP	Treat - ID		Mesocosm	Nitrate [µmol L^{-1}]	Phosphate [µmol L^{-1}]	DIN:DIP	Treat - ID
MK 13	11.2	0.15	76.8	12.0N/0.25P		MK 13	2.1	0.46	4.5	2.0N/0.75P
MK 14	11.2	0.16	69.8	12.0N/0.25P		MK 15	1.9	0.56	3.3	2.0N/0.75P
MK 16	11.3	0.15	75.8	12.0N/0.25P		MK 16	2.7	0.48	5.6	2.0N/0.75P
MK 1	11.5	0.73	15.8	12.0N/0.75P		MK 9	4.6	0.45	10.4	4.0N/0.75P
MK 2	11.0	0.68	16.1	12.0N/0.75P		MK 11	4.5	0.47	9.6	4.0N/0.75P
MK 3	10.6	0.52	20.5	12.0N/0.75P		MK 12	4.0	0.49	8.2	4.0N/0.75P
MK 10	10.8	0.61	17.6	12.0N/0.75P		MK 14	12.6	0.47	27.0	12.0N/0.75P
MK 6	10.7	1.14	9.4	12.0N/1.25P		MK 4	12.4	0.51	24.3	12.0N/0.75P
MK 7	11.2	1.12	9.9	12.0N/1.25P		MK 1	12.6	0.51	24.7	12.0N/0.75P
MK 8	10.9	1.09	10.0	12.0N/1.25P		MK 2	20.6	0.47	43.9	20.0N/0.75P
MK 9	10.5	1.57	6.7	12.0N/1.75P		MK 3	20.6	0.45	45.9	20.0N/0.75P
MK 11	10.8	1.58	6.9	12.0N/1.75P		MK 6	21.9	0.45	48.8	20.0N/0.75P
MK 12	11.1	1.53	7.2	12.0N/1.75P		MK 7	6.7	0.78	8.5	6.0N/1.03P
MK 4	5.7	1.00	5.7	6.35N/1.10P		MK 8	6.9	0.18	39.4	6.35N/0.40P
MK 15	16.9	1.01	16.7	17.65N/1.10P		MK 10	18.5	0.22	84.3	17.65N/0.40P
						MK 5	18.4	0.79	23.4	17.65N/1.10P
Legends	✶	12.0N/0.25P					×	2.00N/0.75P		
	●	12.0N/0.75P					○	4.00N/0.75P		
	▽	5.35N/1.10P					▽	6.00N/1.10P		
	■	17.65N/1.10P					◆	6.35N/0.40P		
	×	12.0N/1.25P					●	12.0N/0.75P		
	△	12.0N/1.75P					✶	17.65N/0.40P		
							■	17.65N/1.10P		
							♀	20.0N/0.75P		

Table 1: Summary of initial conditions of the seawater used to fill the mesocosms during the two experiments, target nutrient concentrations (treat-ID), and different nutrient conditions inside the mesocosms after nutrient addition (day 1).

	Varied P					***Varied N***			
Day 0									
Latitude			16.74°N					16.76°N	
Longitude			25.16°W					25.16°W	
POC [µmol L^{-1}]			13.6 ± 3.8					11.9 ± 1.9	
PON [µmol L^{-1}]			1.85 ± 0.68					1.54 ± 0.26	
POP [µmol L^{-1}]			0.10 ± 0.02					0.07 ± 0.01	
Chl *a* [µg L^{-1}]			0.38 ± 0.09					0.18 ± 0.05	
DOC [µmol L^{-1}]			95 ± 4.6					96± 3.9	
DON [µmol L^{-1}]			8.8 ± 1.1					11 ± 1.5	
Day 1									
Mesocosm	Nitrate [µmol L^{-1}]	Phosphate [µmol L^{-1}]	DIN:DIP	Treat - ID		Mesocosm	Nitrate [µmol L^{-1}]	Phosphate [µmol L^{-1}]	DIN:DIP	Treat - ID
MK 13	11.2	0.15	76.8	12.0N/0.25P		MK 13	2.1	0.46	4.5	2.0N/0.75P
MK 14	11.2	0.16	69.8	12.0N/0.25P		MK 15	1.9	0.56	3.3	2.0N/0.75P
MK 16	11.3	0.15	75.8	12.0N/0.25P		MK 16	2.7	0.48	5.6	2.0N/0.75P
MK 1	11.5	0.73	15.8	12.0N/0.75P		MK 9	4.6	0.45	10.4	4.0N/0.75P
MK 2	11.0	0.68	16.1	12.0N/0.75P		MK 11	4.5	0.47	9.6	4.0N/0.75P
MK 3	10.6	0.52	20.5	12.0N/0.75P		MK 12	4.0	0.49	8.2	4.0N/0.75P
MK 10	10.8	0.61	17.6	12.0N/0.75P		MK 14	12.6	0.47	27.0	12.0N/0.75P
MK 6	10.7	1.14	9.4	12.0N/1.25P		MK 4	12.4	0.51	24.3	12.0N/0.75P
MK 7	11.2	1.12	9.9	12.0N/1.25P		MK 1	12.6	0.51	24.7	12.0N/0.75P
MK 8	10.9	1.09	10.0	12.0N/1.25P		MK 2	20.6	0.47	43.9	20.0N/0.75P
MK 9	10.5	1.57	6.7	12.0N/1.75P		MK 3	20.6	0.45	45.9	20.0N/0.75P
MK 11	10.8	1.58	6.9	12.0N/1.75P		MK 6	21.9	0.45	48.8	20.0N/0.75P
MK 12	11.1	1.53	7.2	12.0N/1.75P		MK 7	6.7	0.78	8.5	6.0N/1.03P
MK 4	5.7	1.00	5.7	6.35N/1.10P		MK 8	6.9	0.18	39.4	6.35N/0.40P
MK 15	16.9	1.01	16.7	17.65N/1.10P		MK 10	18.5	0.22	84.3	17.65N/0.40P
						MK 5	18.4	0.79	23.4	17.65N/1.10P
Legends	✶	12.0N/0.25P					×	2.00N/0.75P		
	●	12.0N/0.75P					○	4.00N/0.75P		
	▽	5.35N/1.10P					▽	6.00N/1.10P		
	■	17.65N/1.10P					◆	6.35N/0.40P		
	×	12.0N/1.25P					●	12.0N/0.75P		
	△	12.0N/1.75P					✶	17.65N/0.40P		
							■	17.65N/1.10P		
							♀	20.0N/0.75P		

1021

Table 2: Mean deviations (MD) from the average development, averaged for each mesocosm for the full experimental period (day 1-day8) and Pearson coefficients for correlations of MD versus initial nutrient concentration [µmol L^{-1}]; bold numbers indicate significant correlation (p<0.05).

Varied P	Chl*a*	Bact	POC	PN	DOC	DON	TEP	CSP	*Varied N*	Chla	Bact	POC	PN	DOC	DON	TEP	CSP
treatment	μL^{-1}	$10^5 L^{-1}$	µM	µM	µM	µM	$10^6 L^{-1}$	$10^5 L^{-1}$	treatment	μL^{-1}	$10^5 L^{-1}$	µM	µM	µM	µM	$10^6 L^{-1}$	$10^5 L^{-1}$
12.0N/0.75P	-0.21	2.84	2.45	0.35	3.81	-0.27	4.42	2.07	12.0N/0.75P	0.15	-1.70	4.24	0.61	3.3	1.1	-6.47	-4.23
12.0N/0.75P	0.03	-0.65	1.93	0.14	-1.39	-0.54	21.16	3.32	12.0N/0.75P	0.23	1.12	4.87	0.56	2.7	-0.6	1.78	14.98
12.0N/0.75P	0.06	-0.69	3.35	0.71	-0.74	0.00	16.00	4.73	12.0N/0.75P	0.64	1.10	11.32	1.34	-0.7	-0.9	5.09	12.60
12.0N/0.75P	0.06	3.61	-0.10	0.29	-4.41	0.19	0.53	-5.63	-	-	-	-	-	-	-	-	-
17.65N/1.10P	0.54	4.14	4.07	0.83	3.15	-0.38	7.77	5.48	17.65N/1.10P	0.76	4.24	2.34	0.75	-1.4	-0.5	-7.40	8.06
12.0N/0.25P	-0.28	-1.44	-8.30	-1.14	-4.86	0.49	-19.47	3.39	2.00N/0.75P	-1.01	-1.58	-4.51	-1.14	-2.3	-0.5	-15.10	-18.80
12.0N/0.25P	-0.26	-0.46	-6.51	-0.99	-4.39	0.56	-17.77	-6.21	2.00N/0.75P	-1.04	-1.89	-14.10	-2.12	-9.3	3.4	-21.78	-19.77
12.0N/0.25P	-0.30	-1.09	-2.00	-0.67	-0.10	0.13	-17.16	-4.46	2.00N/0.75P	1.05	1.85	7.29	1.51	1.5	-0.1	17.43	-1.03
6.35N/1.10P	-0.29	-0.79	-0.47	-0.35	-2.48	-0.51	5.83	-4.87	4.00N/0.75P	-0.62	-0.52	-5.46	-1.05	-3.9	-0.7	1.07	-9.07
12.0N/1.25P	0.03	0.28	4.86	0.58	2.84	-0.41	0.59	0.15	4.00N/0.75P	0.91	-0.79	7.45	1.17	6.2	-0.3	15.35	16.30
12.0N/1.25P	0.16	-0.73	0.39	0.10	5.46	0.24	10.52	-2.35	4.00N/0.75P	-0.22	-0.79	-6.56	-1.54	-2.4	-1.6	3.12	-9.56
12.0N/1.25P	0.38	-1.32	2.71	0.19	4.69	0.06	6.48	-6.93	6.00N/1.03P	-0.65	-2.14	-12.28	-1.73	-0.1	-1.3	-23.60	-8.95
12.0N/1.75P	0.13	-2.16	-1.61	-0.40	-2.89	0.04	3.00	4.16	6.35N/0.40P	-1.09	-2.20	-8.85	-1.38	-18.8	-2.2	-15.68	-14.42
12.0N/1.75P	-0.27	-0.83	-4.35	-0.19	4.07	-0.12	-15.74	4.07	17.65N/0.40P	1.31	1.30	14.47	2.76	4.2	0.8	33.98	24.11
12.0N/1.75P	0.23	-0.70	1.66	0.26	-2.75	0.51	-6.15	3.07	20.0N/0.75P	-0.49	1.26	0.10	-0.25	0.5	0.1	-5.21	-0.84
									20.0N/0.75P	-0.88	-0.88	-10.83	-1.58	-4.8	0.3	-21.95	-9.19
									20.0N/0.75P	0.94	1.62	10.52	2.08	7.7	1.8	39.38	19.81
$r(PO_4^{3-})$ =	**0.45**	-0.10	0.37	0.41	0.39	-0.24	0.25	0.31	r (NO_3^-)=	**0.97**	**0.70**	**0.87**	**0.94**	**0.71**	0.18	**0.80**	**0.86**

1022
1023

Table 3: Statistics for linear regression analysis of gel particle numerical abundance and DOC concentration against organic matter components during mesocosm experiments with different initial PO_4^{3-} (*Varied P;* µmol L^{-1}) and NO^{3-} (*Varied N;* µmol L^{-1}) concentrations. Units TEP: x10^7 L^{-1}, CSP: x10^6 L^{-1}, POC: µmol L^{-1}, PN: µmol L^{-1}, Chl *a* : µg L^{-1}, DOC µmol L^{-1}, bacteria x10^6 mL^{-1} . *a* is the slope and *b* is the intercept. See figure 7 for further information.

Formatiert: Schriftart: Kursiv

Formatiert: Schriftart: Kursiv

	Varied P				***Varied N***			
	a	*b*	n	r^2	*a*	*b*	n	r^2
TEP vs.								
Chla	2.0±0.22	1.27±0.39	60	0.65	1.2±0.08	1.52±0.26	96	0.69
POC	0.18±0.012	-0.63±0.49	89	0.72	0.22±0.13	-1.5±0.60	128	0.70
PN	1.2±0.07	-1.4±0.4	89	0.80	1.5±0.1	-1.2±0.7	128	0.64
DOC	0.14±0.02	-8.7±2.2	90	0.34	0.22±0.02	-18±2.1	127	0.54
bacteria	3.4±0.4	0.78±0.67	90	0.46	6.8±0.9	-1.3±1.1	128	0.32
CSP vs.								
Chla	1.3±0.1	1.4±0.3	60	0.76	2.5±0.15	3.2±0.5	96	0.74
POC	0.11±0.01	0.3±0.4	89	0.58	0.25±0.01	-1.2±0.6	112	0.77
PN	0.7±0.06	0.2±0.3	89	0.65	1.9±0.09	-0.1±0.6	112	0.80
DOC	0.10±0.01	-6.6±1.4	90	0.42	0.21±0.03	-13±3.0	111	0.35
bacteria	2.3±0.26	0.63±0.43	90	0.49	8.8±0.84	-2.3±1.11	128	0.47
DOC vs								
Chla	*n.s*	-	-	-	*n.s.*	-	-	-
POC	0.54±0.06	88±2	119	0.38	0.66±0.05	88±2	127	0.58
PN	3.5±0.4	88±2	119	0.38	4,2±0.4	90±3	127	0.47
bacteria	11±1.5	92±2	119	0.31	21±3.1	88±4	127	0.27

Table 4: Ratios of estimated carbon content of transparent exopolymer particles (TEP-C) to concentrations of particulate organic carbon (POC), total organic carbon (TOC), particulate nitrogen (PN) and Chl *a* ~~concentrations~~. Average values (mean for TEP-C, median for ratios) are given for replicate treatments on day 1 and 8 during *Varied P* and *Varied N*, respectively.

Sampling	*n*	Treat_ID	TEP-C [µmol L^{-1}]	TEP-C : POC [mol %]	TEP-C : TOC [mol %]	TEP-C : PN [mol:mol]	TEP-C : Chl *a* [µM:µg L^{-1}]
Varied P							
Day 1	3	12.0N/0.25P	0.52	3.01	0.48	16.3	0.25
1	4	12.0N/0.75P	0.40	3.12	0.36	3.4	0.26
1	1	6.35N/1.10P	0.98	5.98	0.83	13.0	0.45
1	1	17.65N/1.10P	0.52	4.14	0.45	7.5	0.28
1	3	12.0N/1.25P	0.49	3.99	0.46	4.7	0.29
1	3	12.0N/1.75P	0.55	5.12	0.50	4.4	0.38
Day 8	3	12.0N/0.25P	13	41	8.4	2.21	25
8	4	12.0N/0.75P	16	15	10.4	2.62	28
8	1	6.35N/1.10P	21	28	14.8	2.85	63
8	1	17.65N/1.10P	22	31	13.3	2.77	61
8	3	12.0N/1.25P	18	26	9.9	2.79	32
8	3	12.0N/1.75P	35	19	17.6	3.63	83
Varied N							
Day 1	3	2.0N/0.75P	0.36	3.07	0.29	0.21	2.04
1	3	4.0N/0.75P	0.62	4.90	0.54	0.36	3.84
1	1	6.0N/1.03P	0.50	4.99	0.48	0.41	4.18
1	1	6.35N/0.40P	0.51	4.56	0.47	0.35	3.63
1	3	12.0N/0.75P	0.88	7.34	0.90	0.66	5.16
1	1	17.65N/0.40P	1.77	14	1.67	1.12	9.33
1	1	17.65N/1.10P	0.97	9.32	0.91	0.66	7.43
1	3	20.0N/0.75P	0.75	4.86	0.68	0.40	4.37
Day 8	3	2.0N/0.75P	25	52	12.0	3.42	47
8	3	4.0N/0.75P	46	82	22.4	6.61	48
8	1	6.0N/1.03P	35	87	18.9	6.88	36
8	1	6.35N/0.40P	37	53	17.3	4.03	45
8	3	12.0N/0.75P	40	43	15.6	3.51	43
8	1	17.65N/0.40P	68	93	29.1	6.36	81
8	1	17.65N/1.10P	23	26	9.7	1.79	14
8	3	20.0N/0.75P	42	47	16.1	3.16	19

Figure captions:

Fig. 1, a-f: Bloom development during two series of mesocosms experiments with varied supply of PO_4^{3-}(*Varied P;* a, c, e; *n*=16) or NO_3^- (*Varied N;* b, d, f*; n*=16), respectively. Shaded areas indicate the range (min-max) of data observed during both treatments for Chl *a* concentration (a, b), bacterial abundance (c, d) and particulate organic carbon (POC) concentration (e, f).

Fig. 2, a-d: Nutrient concentrations during two series of mesocosm experiments with varied supply of PO_4^{3-} (*Varied P;* a, c; *n*=16) or NO_3^- (*Varied N;* b, d; *n*=16)), respectively. For treatments with identical nutrient supply, average values are given ±1 standard deviation (error bars). See table 1 for explanation of symbols.

Fig. 3, a-d: Changes in dissolved organic carbon (ΔDOC; a, b) and dissolved organic nitrogen (ΔDON; c, d) concentration during *Varied P* (a, c) and *Varied N* (b, d). Values are given as difference to day 1. For treatments with identical nutrient supply, average values are given ±1 standard deviation (error bars). The dashed line visualizes the zero value; symbols as in Table 1.

Fig. 4, a-d: Temporal changes in the total numerical abundance of transparent exopolymer particles (TEP; a, b) and of Ceoomassie stainable particles (CSP; c, d) during *Varied P* (a, c) and *Varied N* (b, d). For treatments with identical nutrient supply, average values are given ±1 standard deviation (error bars). The dashed line visualizes the zero value; symbols as in Table. 1.

Fig. 5, a-d: Size frequency distribution of gel particles. Calculation of the size frequency distribution slope exemplified for TEP, averaged for all mesocoms on day 1 (circles) and 8 (triangles) during *Varied P* (lefta) and *Varied N* (rightb), respectively and for CSP on day 2

(circles) and 8 (triangles) during *Varied P* (c) and *Varied N* (d). Linear regression of log[$dN/d(d_p)$] versus log[d_p] was fitted to the particles in the size range of 1.05 – 14.14 µm ESD (solid symbols).

Fig. 6, a-d: Changes in the slope (δ) of the size frequency distribution of TEP (a, b) and CSP (c, d) during the mesocosm blooms. The grey lines indicate the mean value of all mesocosms on the respective day; symbols as in Table 1.

Fig. 7, a-i: Relationships between organic components during *Varied P* and *Varied N*. Solid symbols: data obtained during *Varied P;* open symbols: data obtained during *Varied N*. Linear regressions with Chl *a* include data of samplings 1, 2 and 5 for *Varied P* and 1-6 for *Varied N*~~6~~. Linear regressions with POC and PN include data of all samplings. Information on regression statistics is given in table 2.

Fig. 8, a-b: The maximum numerical abundance of TEP (a) and CSP (b) in the mesocosms increased with the initial (day 1) [DIN]:[DIP] ratio during *Varied N* (open symbols), but not during *Varied P* (solid symbols).

Fig 9, a-c: Comparison of Chl *a* concentration (a), accumulation of DOC (b, open symbols) and DON (b, solid symbols), and abundance of TEP (c, open symbols) and CSP (c, solid symbols) observed in the course of the two mesocosms experiments for the treatment 12.0N/0.75P. Direct relationships ([$y_{Varied\ N}$] = a [$x_{Varied\ P}$]+b) were observed for Chl *a,* with a=2.3±0.2, r^2=0.94, n=8; DOC with a=2.1±0.4, r^2=0.84, n=8, TEP with a= 1.7±0.4, r^2=0.78, n=6 and CSP with a=3.3±0.7, r^2=0.86, n=6. Symbols represent mean values of 3 mesocosms (*Varied P*) or 4 mesocosms (*Varied N*) with ± 1 standard deviation (error bars).

Formatiert: Schriftart: Kursiv
Formatiert: Schriftart: Kursiv
Formatiert: Schriftart: Kursiv
Formatiert: Schriftart: Kursiv

Figures:

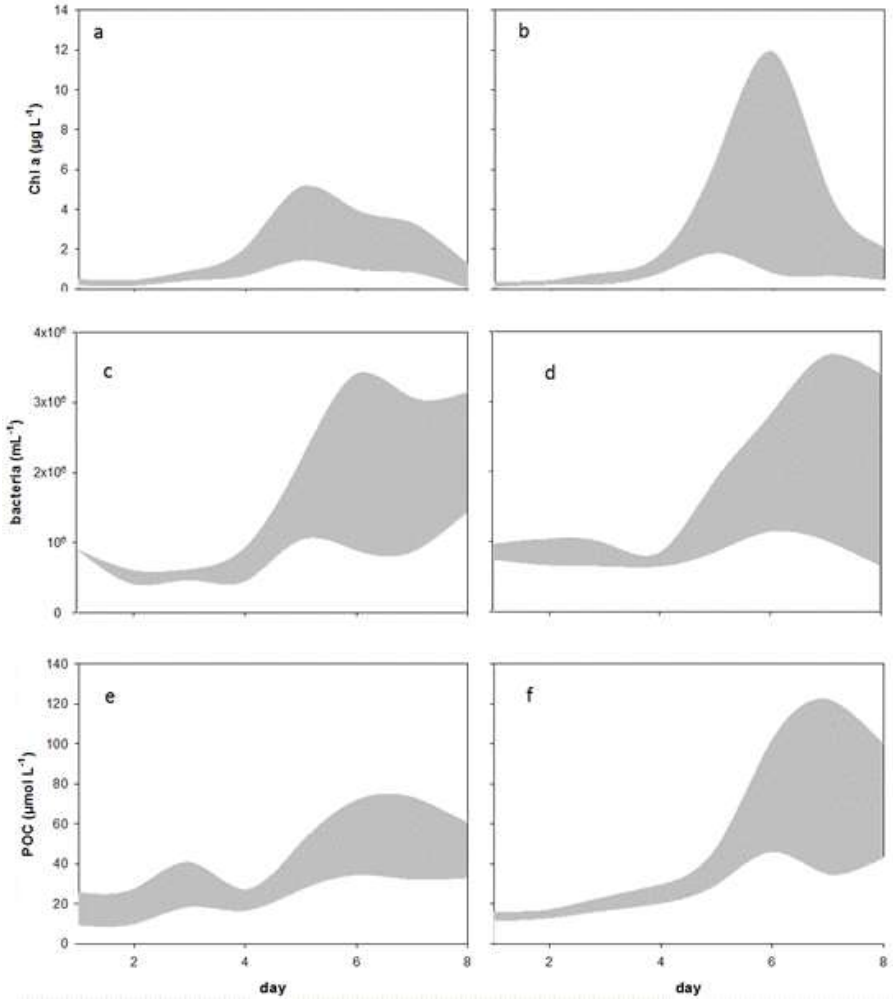


Figure: 1, a-f

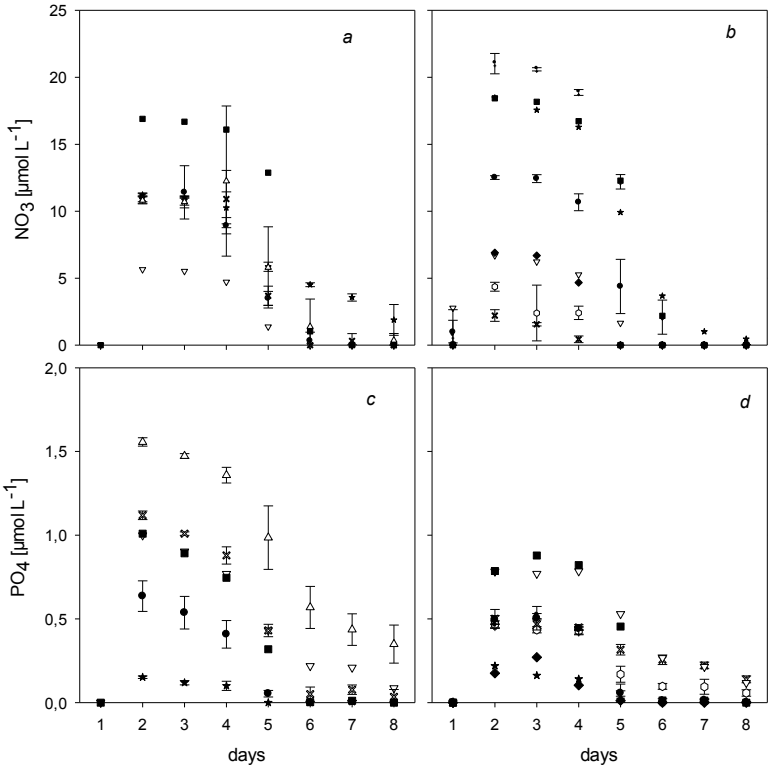


Figure: 2, a-d

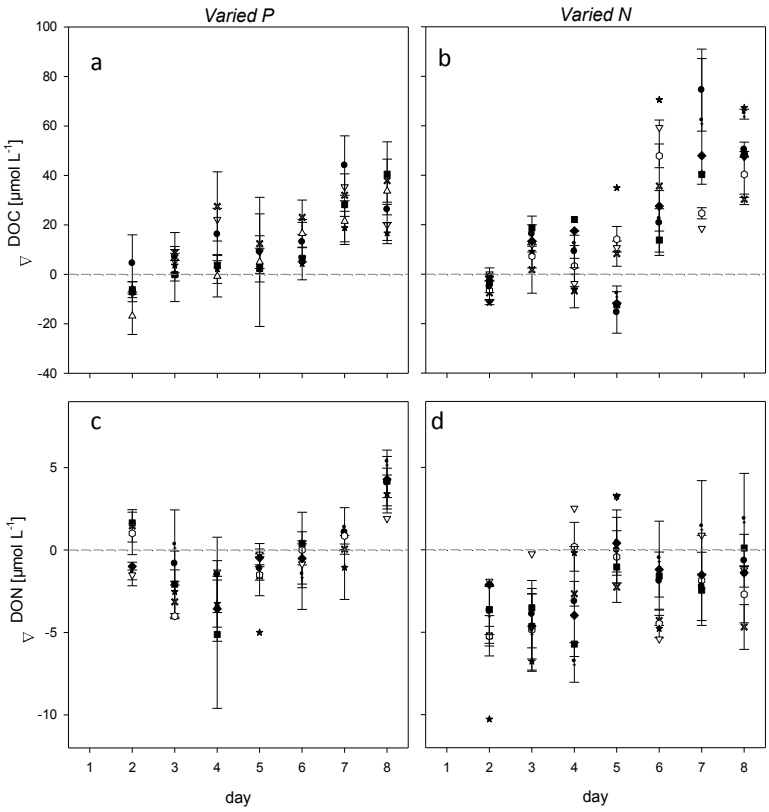


Figure: 3, a-d

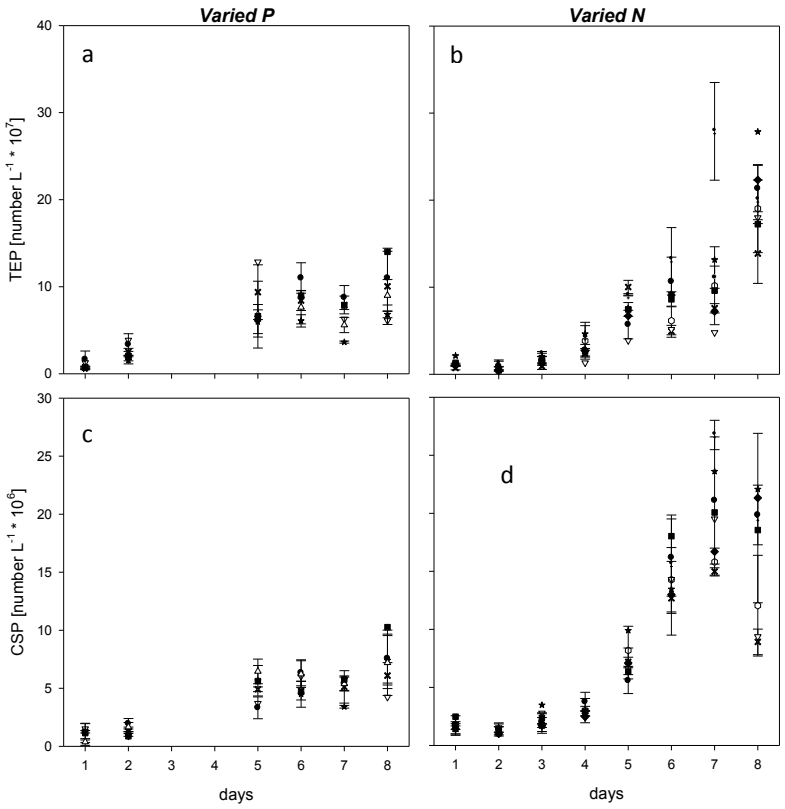
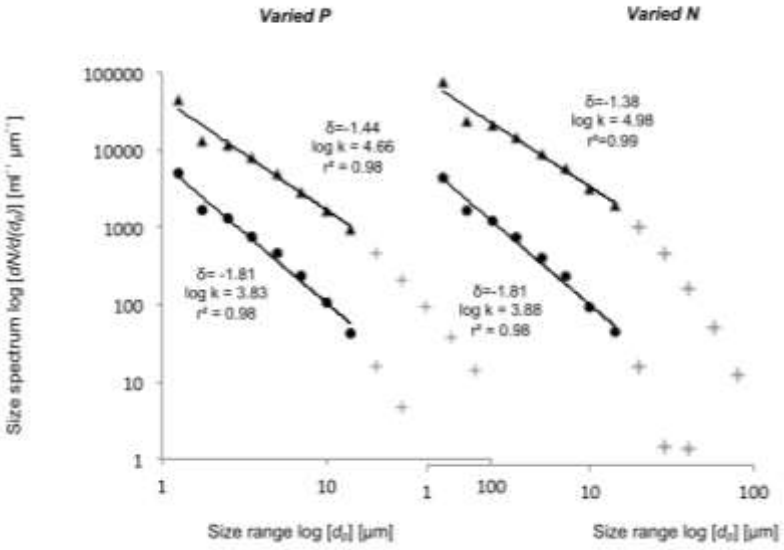

Varied P
Varied N
a
b
c
d
TEP [number L-1 * 10^7]
CSP [number L-1 * 10^6]
days
days

Figure: 4, a-d


Varied P
Varied N
100000
10000
1000
100
10
1
δ=-1.44
log k = 4.66
r² = 0.98
δ= -1.81
log k = 3.83
r² = 0.98
δ=-1.38
log k = 4.98
r²=0.99
δ=-1.81
log k = 3.88
r² = 0.98
1
10
1
100
10
100
Size spectrum log [dN/d(d_p)] [ml⁻¹ µm⁻¹]
Size range log [d_p] [µm]
Size range log [d_p] [µm]

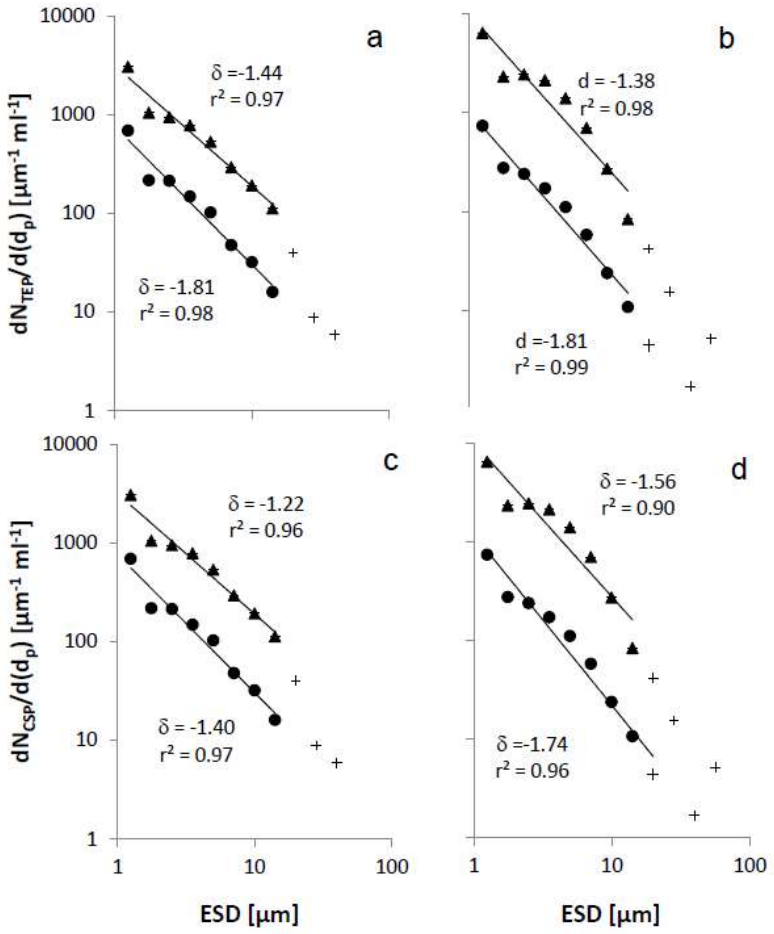


Figure: 5

Formatiert: Schriftart: Fett

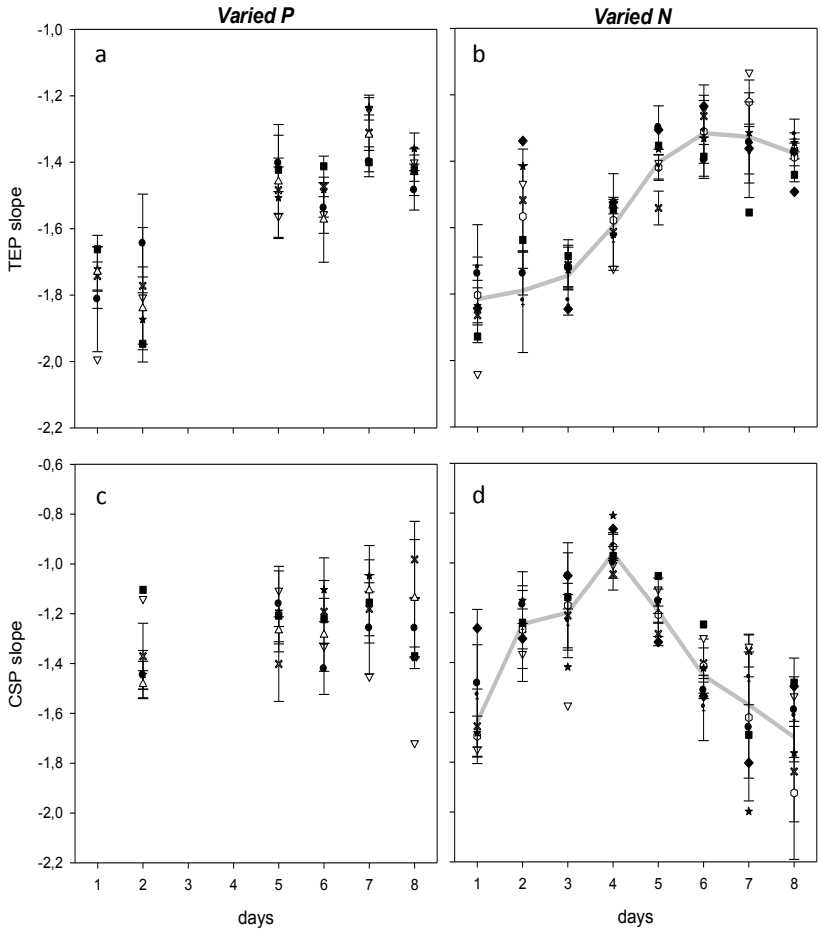

Varied P
Varied N
a
b
c
d
TEP slope
CSP slope
-1,0
-1,2
-1,4
-1,6
-1,8
-2,0
-2,2
-0,6
-0,8
1
2
3
4
5
6
7
8
days

Figure: 6, a-d

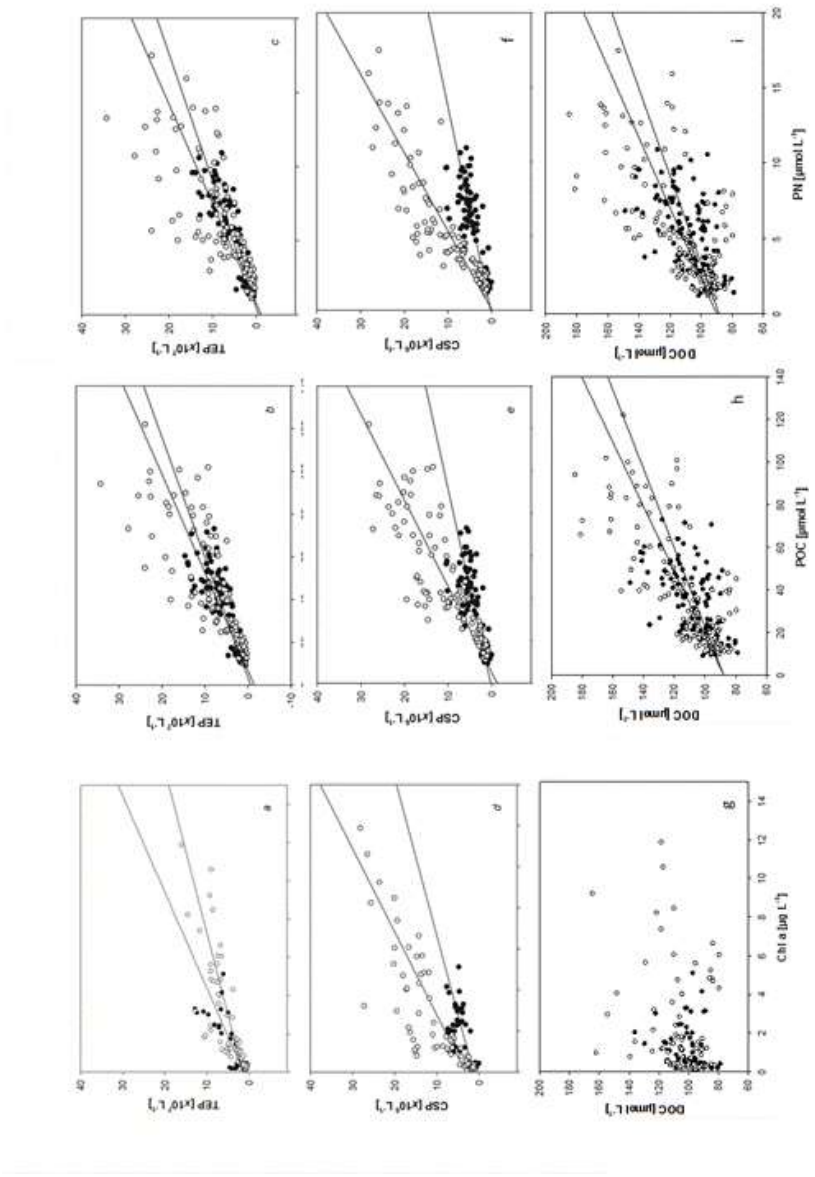
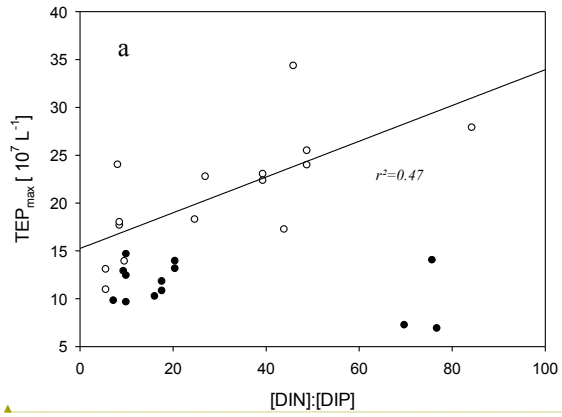

a
b
c
d
e
f
g
h
i
TEP [x10⁶ L⁻¹]
CSP [x10⁶ L⁻¹]
DOC [µmol L⁻¹]
Chl a [µg L⁻¹]
POC [µmol L⁻¹]
PN [µmol L⁻¹]

Figure: 7, a-i



~~r^2=0.66~~

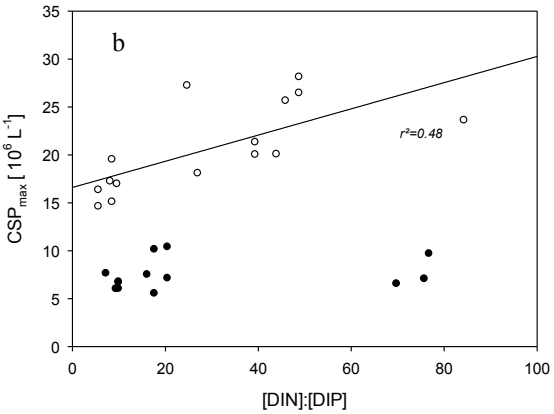


Figure: 8a, b

Formatiert: Schriftart: Fett

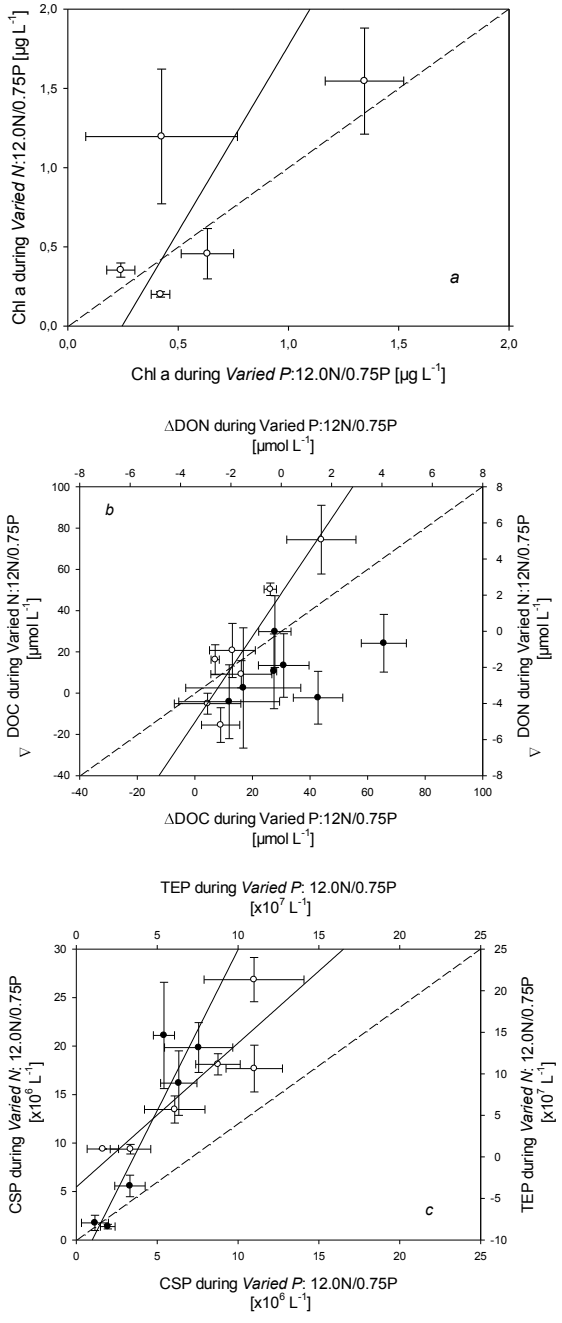

Chl a during *Varied N*:12.0N/0.75P [µg L^{-1}]
Chl a during *Varied P*:12.0N/0.75P [µg L^{-1}]
a
ΔDON during Varied P:12N/0.75P [µmol L^{-1}]
DOC during Varied N:12N/0.75P [µmol L^{-1}]
Δ
DON during Varied N:12N/0.75P [µmol L^{-1}]
Δ
b
ΔDOC during Varied P:12N/0.75P [µmol L^{-1}]
TEP during *Varied P*: 12.0N/0.75P [x10^{7} L^{-1}]
CSP during *Varied N*: 12.0N/0.75P [x10^{6} L^{-1}]
TEP during *Varied N*: 12.0N/0.75P [x10^{7} L^{-1}]
c
CSP during *Varied P*: 12.0N/0.75P [x10^{6} L^{-1}]

Figure: 9, a-c