Master Thesis

Christian-Albrechts-Universität zu Kiel
M.Sc. Biological Oceanography

Temporal development in N-P-Si elemental pools during simulated artificial upwelling

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Submitted in September 2018

Declaration of authorship

I, Moritz Baumann, hereby declare that I am the sole author of the submitted Master's thesis, which was composed under the supervision of

Prof. Ulf Riebesell and Dr. Jan Taucher.

I further declare that I have not used any sources other than those listed in the bibliography and identified as references.

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List of abbreviations

Most important response parameters:

- ΔDIM: consumed dissolved inorganic matter
- EP: export potential
- NCP: net community production
- NEP: nutrient export potential
- NUE: nutrient utilisation efficiency

Further biogeochemical and biological parameters:

- BSi: biogenic silica
- C, N, P, Si: carbon, nitrogen, phosphorus, silicon
- CDOM: chromophoric dissolved organic matter
- Chl *a*: chlorophyll a
- DIC, DIN, DIP, DSi: dissolved inorganic C, N, P, dissolved silica
- DIM: dissolved inorganic matter
- DMS, DMSP: dimethyl sulfide, dimethylsulfoniopropionate
- DOC, DON, DOP: dissolved organic C, N, P
- DOM: dissolved organic matter
- pCO_2: CO_2 partial pressure
- PIC, PIN, PIP: particulate inorganic C, N, P
- PM (PM_{susp}, PM_{sed}) particulate matter (suspended, sedimented)
- POC, PON, POP: particulate organic C, N, P
- TA: total alkalinity
- TPC, TPN, TPP: total particulate C, N, P

Others:

- ANOVA: analysis of variance
- BCP: biological carbon pump
- CFA: continuous flow analyser
- CRM: certified reference material
- CTD: conductivity, temperature, depth
- DOW: deep ocean water

- EE: export efficiency
- IUPAC: International Union of Pure and Applied Chemistry
- KOSMOS: Kiel Off-Shore Mesocosms for Oceanographic Studies
- LOD: limit of detection
- M1-M8: mesocosm 1-8
- MilliQ: type 1 purified water
- NA: nutrient addition
- OM: organic matter
- OTEC: ocean thermal energy conversion
- PAR: photosynthetically active radiation
- PP: primary production
- SD: standard deviation
- SST: sea-surface temperature
- t0-t30: experimental day 0-30
- TTE: trophic transfer efficiency

1 Abstract

Overpopulation and climate change are two major socio-economic threats to humanity. Finding new sources of sustainable food production, as well as reducing the anthropogenic net carbon dioxide emissions are necessary steps to face these challenges. Artificial upwelling is a concept that addresses these topics, as its applications are fish production and atmospheric CO_2 sequestration. It means bringing up deep ocean water to fertilize oligotrophic upper ocean waters and thus increase productivity. However, the consequences of artificial upwelling are yet poorly understood. In this study, the responses of a pelagic system to different rates of artificially added inorganic nutrients are determined for the nitrogen (N), phosphorus (P) and silicon (Si) elemental pools. The objectives are the examination of the relationship between the rate of nutrient supply and the export efficiency as well as the efficiency of nutrient utilisation.

Therefore, a four-week mesocosm experiment was conducted on the isle of Gran Canaria from August to October 2017 as part of the Ocean artUp project. Eight mesocosms were filled with oligotrophic surface water. Inorganic nutrients (nitrate, phosphate, and silicic acid) were added daily at three different rates (low, medium, high) with an Si:N:P ratio of 8:16:1. A wide range of biogeochemical and biological parameters was estimated each day, including dissolved inorganic and organic nutrients, particulate matter, sedimented matter, and phyto- and zooplankton biomass and abundances. Mass balances were estimated for N, P, and Si. Additionally, net community production, nutrient utilisation efficiency, and export potential were determined.

Most of the assessed mass balances did not add up. It is assumed that this is mainly due to the highly problematic dissolved organic nutrient and sedimented matter data. We found that the higher the rate of nutrient addition, the higher the productivity. Nutrient utilisation was lowest in the high treatment level. This was due to its high productivity, which resulted in CO_2 limitation early on. Export potential was highest in the low and high treatments, and lowest in the medium treatment. It seems likely that export potential would have increased in the medium treatment at a longer experimental duration.

The results of this study imply that the rate of nutrient addition of the high treatment level is feasible in terms of efficient carbon export, while a rate of nutrient addition near the medium treatment level seems to be more advisable for pelagic fish production. Furthermore, methodological revisions for dissolved organic nutrient and sedimented matter measurements are proposed, as well as specifications of experimental setups for further artificial upwelling research. This study makes an important contribution to the Ocean artUp project by providing

novel information on biogeochemical implications of different rates of simulated artificial upwelling.

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2 Introduction and Literature Review

2.1 Artificial upwelling

Two main challenges of our modern societies are overpopulation and climate change. This implies major regulations for human kind: we need to strictly cut down carbon dioxide emissions and provide more forms of sustainable energy (Fuss et al., 2014; Le Quéré et al., 2009), and we need to create more sustainable food production to feed an ever-growing population (Godfray et al., 2010). The oceans have been serving mankind in buffering CO_2 emissions ever since the beginning of the industrial era with ocean acidification being one of the consequences (Khatiwala et al., 2009; Sabine et al., 2004; Siegenthaler and Sarmiento, 1993). They also form a major repertoire of food provision, but fishing down of marine food webs (Pauly, 1998) is not a way of sustainable food supply. Besides better management of fisheries and less fish consumption, what is needed, are more productive ocean regions that can be used for fish production in a sustainable way.

Productivity in surface ocean waters is mainly regulated by the availability of light and nutrients. The main physical factor controlling the light and nutrient regimes in the upper ocean layer is vertical mixing (Lewis et al., 1986; Sverdrup, 1953). The degree of vertical mixing in the open ocean is mainly governed by wind turbulence and the sea-surface temperature (SST). Climate change has been causing SSTs to increase since the beginning of the 20th century (Cane et al., 1997; Huang et al., 2017), inducing stronger stratification in the upper ocean, and thus a decline in nutrient-supply from deep water mixing (Sarmiento et al., 2004). According to Behrenfeld et al. (2006), permanently stratified ocean regions which experience elevated SST will also experience reduced productivity. Therefore, the ocean's most oligotrophic waters located in the areas of the subtropical gyres, commonly referred to as ocean deserts, are expanding with climate change (Irwin and Oliver, 2009; Polovina et al., 2008). There are approaches that aim at fertilizing these low productive surface waters of oligotrophic ocean regions to increase productivity of pelagic fish.

One concept with the potential to fertilize parts of these vast oligotrophic regions is called artificial upwelling. By bringing up cold, nutrient-rich deep ocean water (DOW) into the upper sunlit water layer, which is generally warmer and scarce in nutrients, productivity is stimulated. Wind-driven upwelling in coastal areas usually has the effect of enhancing primary production (Falkowski, 1998; González-Rodríguez et al., 2012; Walsh et al., 1978; Zaytsev et al., 2003)

and the same effect has been reported by multiple studies carrying out artificial upwelling experiments (Aure et al., 2007; Giraud et al., 2016; Handå et al., 2013; McAndrew et al., 2007; McClimans et al., 2010; Strohmeier et al., 2015). The technique has the potential to significantly enhance biological productivity of oligotrophic systems.

Increased production from artificial upwelling could be a way of helping to solve the problems arising with overpopulation and to face the challenges that come along with climate change. One of the three main applications of artificial upwelling is ecosystem-based fish farming. By enhancing the productivity of primary producers, the potential food supply for higher trophic levels, up to small pelagic fish species and beyond, increases. Cury and Roy (1989) proposed that the relationship between recruitment of small pelagic fish and upwelling intensity of non-Eckman-type upwelling is linear. Artificial upwelling therefore could be a sustainable way of enhancing mariculture, i.e. the cultivation of marine organisms in the open ocean, by producing small pelagic fish and/or shellfish. Early studies investigating this topic found that it is feasible to rear chum salmon fry (Paul et al., 1976) or accelerate the growth of *Mytilus edulis* (Paul et al., 1978) in an artificial upwelling pond. A more recent study by Strohmeier et al. (2015) concluded that mussel growth performance, as well as the cultured biomass that can be sustained by available food, can be enhanced by sustained artificial upwelling.

Another application may be the fertilization-induced sequestration of atmospheric CO_2 in the deep ocean. The idea being that, due to enhanced primary production (PP) in an oligotrophic system, additional carbon dioxide is photosynthetically fixed as organic carbon, part of which is then exported to and stored in the deep ocean (Lovelock and Rapley, 2007). This causes a decline in surface ocean pCO_2 and therefore a net flux of atmospheric CO_2 into the ocean. One problem with this approach is that DOW is rich in inorganic carbon, meaning that many regions might even be net sources of CO_2 to the atmosphere when experiencing upwelling rather than sinks (Shepherd et al., 2007). Oschlies et al. (2010) conducted a modelling study in which they investigated the potential of long-term pipe-induced artificial upwelling for anthropogenic carbon sequestration on a global scale. They state that, under the most optimistic assumptions, the global sequestration potential would account for 0.9 Pg C yr^{-1}. This is a relatively small number compared to the global anthropogenic carbon dioxide emissions of more than 9.55 Pg C yr^{-1} in the year 2010 (Pachauri et al., 2014). Interestingly, most of that carbon (~80%) would be stored on land, because the cold, upwelled waters would cause decreasing air temperatures, resulting in reduced respiration on land. And, when upwelling is stopped after a couple of decades, surface temperatures and atmospheric CO_2 concentrations would

subsequently rise to concentrations even higher than in their control scenarios. There are many more model-based estimates of possible CO_2 drawdowns of artificial upwelling approaches, all of them suggesting major uncertainties when it comes to the practicability for sequestration of atmospheric carbon (Bauman et al., 2014; Keller et al., 2014; Lenton and Vaughan, 2009; Williamson et al., 2009; Yool et al., 2009). However, to date there are few artificial upwelling experiments which investigate the vertical flux of organic matter (OM) and thus the export potential (e.g. Svensen et al., 2002).

The third application of artificial upwelling is the production of renewable energy. In so called OTEC (ocean thermal energy conversion) power plants the thermal gradient between surface and deep ocean water is used to generate electrical power (Fuller, 1978). However, since the technology is neither economically nor technically feasible yet, commercially used OTEC plants remain hypothetical. Fujita et al. (2012) argue though that the urgency for them is rising as the necessity of new forms of renewable energy increases.

Although artificial upwelling has received considerable attention in the past decades, the effects of prolonged artificial upwelling on pelagic communities remain unknown. How efficiently are upwelled nutrients utilised and exported? What effect does the upwelling intensity have on these parameters? To assess the biogeochemical consequences of potential large-scale artificial upwelling, fundamental research on the community and ecosystem levels is needed.

2.2 Underlying parameters

Primary producers do not only transform light into chemical energy, they also take up dissolved inorganic carbon (DIC) and incorporate it into dissolved and particulate organic matter (DOM and POM). This organic matter is produced in the surface ocean, and exported to the deep ocean via particle flux, vertical migration of zooplankton, and physical processes such as subduction. During the export and in the deep ocean, organic carbon is respired back to CO_2 by bacteria and archaea performing remineralization. The process of transporting organic carbon from surface waters to the ocean interior is called the 'biological carbon pump' (BCP). The BCP constitutes one of the major planetary C fluxes (Henson et al., 2011), and facilitates the sequestering of atmospheric CO_2 in the deep ocean. The ocean represents a huge sink for anthropogenic CO_2 by taking up around one third of anthropogenic CO_2 emissions every year (Sabine et al., 2004) and thus acting as a buffer for global warming. Without the BCP, atmospheric CO_2 concentrations of ~ 400 ppm in 2015 would have been approximately 50% higher (Parekh et al., 2006).). Therefore, whatever controls the export of organic carbon in the

ocean has a direct effect on CO_2 sequestration and thus indirectly also on the rate of global warming.

The particle flux of organic matter (OM) is a passive, gravitational form of transport, which is made up of marine snow particles. These mainly consist of dead phytoplankton cells and zooplankton faecal pellets. The proportion of total PP that is exported from the euphotic zone is regarded as the export efficiency (EE) (Henson et al., 2011). Thereby, total PP is the sum of new and regenerated production (Dugdale and Goering, 1967). EE is described by the e-ratio:

$$e - ratio = \frac{export\ flux}{PP} \quad (1)$$

Most of the OM export, however, is decomposed and remineralized in the mesopelagic zone (between the euphotic zone and 1,000 m depth), and only a small fraction of what starts sinking out actually reaches the deep ocean (~10 %) (Robinson et al., 2010). This fraction of OM that makes it to the deep ocean (> 1,000 m) is described by the transfer efficiency (Henson et al., 2011). The amount of OM that is exported is subject to strong seasonal (Lampitt et al., 2010) and regional variabilities (Henson et al., 2012), and is directly controlled by the sinking velocity of particles, which is in turn dependent on the particle size (according to Stokes's law), and the rate of particle decay (Kwon et al., 2009). Consequently, high primary production and high export efficiency are required to obtain a pelagic system with the capability to export high amounts of carbon from the euphotic zone. Both of these parameters can potentially be enhanced by artificial upwelling as a form of nutrient enrichment.

2.3 Nutrient cycling of N, P, Si

Primary producers take up inorganic nutrients from the environment, incorporate them into biomass and thus make them available for higher trophic levels. The most important macronutrients limiting primary production in marine systems are nitrogen (N) and phosphorus (P). Nitrogen is necessary e.g. for the synthesis of proteins, while phosphorus is among others needed for nucleotides and phospholipids.

Inorganic nitrogen in the marine realm exists as dissolved nitrogen gas (N_2), ammonium (NH_3/NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-). N_2 gas can be considered an unlimited source of nitrogen for marine organisms in the euphotic zone since it is replenished from the atmosphere via air-sea gas exchange. However, it is not an easily accessible form of N, as a special enzyme is required for the reduction of N_2 to ammonium. A diverse set of prokaryotes, called diazotrophs, is able to perform this nitrogen fixation and can thus thrive where other forms of inorganic nitrogen are not available. Ammonium is the form of inorganic nitrogen that primary

producers take up preferably. This is because the assimilation of N into amino acids requires ammonium as N source (McCarthy et al., 1977; Millero, 2013). Ammonium, however, is much less abundant in the ocean than nitrate. The oceanic inventories of NH_4^+ and NO_3^- are 0.34 Pg N and 580 Pg N, respectively (Gruber, 2008). This is why most autotrophic marine organisms possess the enzymes nitrate reductase and nitrite reductase for assimilating nitrate and nitrite, respectively. Inorganic nitrogen is taken up as one form or the other in surface waters and is either emitted there as ammonium by excretion, viral lysis or direct exudation, and taken up again by microbes fuelling regenerated production (Dugdale and Goering, 1967), or exported from the euphotic zone as dissolved or particulate organic nitrogen (DON or PON). In this case, the organic nitrogen is converted back to ammonium by heterotrophic prokaryotes in a process called ammonification. The organisms thereby use the oxidation of organic carbon to CO_2 to yield energy. The ammonium can then be oxidized by chemoautotrophic prokaryotes to nitrite and subsequently to nitrate.

The phosphorus cycle is less complicated compared to the nitrogen cycle since there is only one form of dissolved inorganic phosphorus (DIP), i.e. phosphate (PO_4^{3-}). The main source of P to the oceans is riverine runoff, while its main sink is sediment burial. Dissolved organic phosphorus (DOP) is often more abundant in surface waters than DIP. Phosphorus is assimilated into biomass in the surface ocean and exported to the deep, where it is remineralized to its inorganic form similar to C and N. Therefore, phosphate is more abundant than DOP in deep waters. The cycling of N and P in a pelagic ecosystem is illustrated in Fig 2.1.

Phosphorus is considered to be the limiting nutrient in the oceans on a geological timescale, since its only sources to the ocean are terrestrial weathering, land-based aerosols, or replenishment from the sediments. Nitrogen on the other hand has a nearly unlimited source to the ocean as N_2 gas via air-sea gas exchange. On a short timescale however, nitrogen is often the limiting nutrient. Firstly because N_2 gas is only available to diazotrophs, secondly because N-fixation can be limited by iron which is required for the N-fixing enzyme, and lastly because N is needed in larger quantities than P for biomass build up.

Another element that is important for nutrient cycling of marine ecosystems is silicon. It occurs as silicic acid in the oceans and is taken up by certain plankton groups such as diatoms, silicoflagelates and radiolarians. They use dissolved silica (DSi) to build up cell structures made of biogenic silica (BSi), also referred to as opal. Diatoms are especially important for biogeochemical nutrient cycling in the ocean. They are bloom-forming organisms that often outcompete all other primary producers, given that inorganic nutrients, especially DSi, are abundant (Egge and Aksnes, 1992). They may account for 25 % of global CO_2 fixation

(Falkowski, 1998) and for 20 % of global net primary production (Mann, 1999). Silicon is not only important in terms of productivity though, but also in connection to the biological carbon pump. The density of BSi is about twice as high as that of organic matter, BSi thus acts as ballast for the export of organic matter (Klaas and Archer, 2002). DSi is supplied to the oceans via riverine runoff and recycling of the relatively fast dissolving BSi. It is taken out of the oceanic system by sediment burial, similar to phosphate.

Nutrient cycling and stratification of the upper ocean as in subtropical regions, generally causes high concentrations of biogenic material (DOM, POM, BSi) and low concentrations of dissolved inorganic nutrients (DIM) in the surface ocean, while biogenic material is remineralized and inorganic nutrient concentrations increase with depth. When bringing up DOW rich in inorganic nutrients, one way to trace the utilisation and cycling of the upwelled nutrients is assessing the different dissolved and particulate nutrient pools of the most important macronutrients C, N, P, and Si. These nutrients can be used as 'currencies' to assess ecological and biogeochemical parameters. For instance: how much N is exported for each N that is added via artificial upwelling? Macronutrients can thus be used to assess the rate of primary production and export efficiency of pelagic communities, as well as the efficiency of trophic transfer in their food chains.

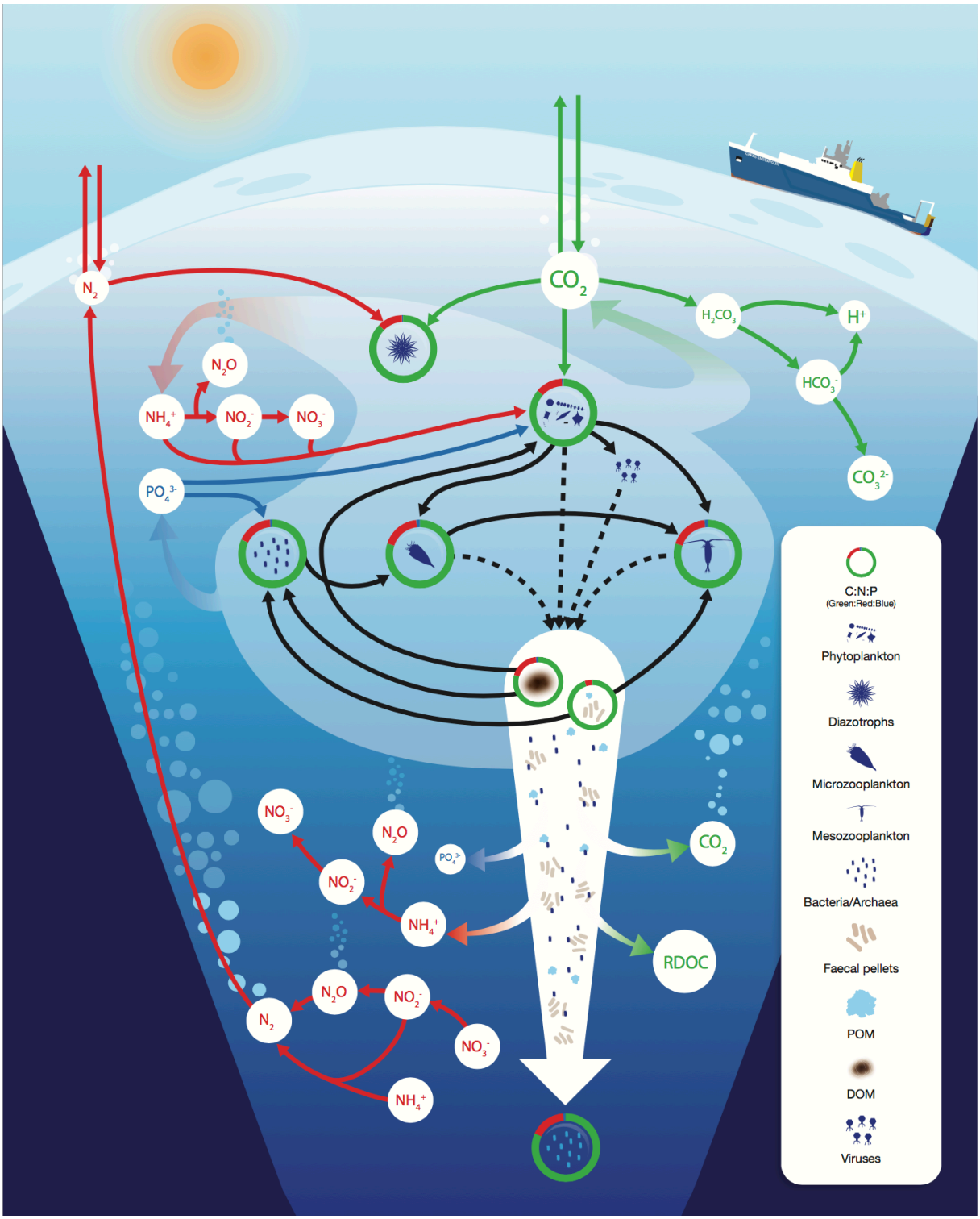


Fig 2.1: **Interactions between the marine biogeochemical cycles of carbon, nitrogen and phosphorus**. Figure by Robinson et al. (2015).

2.4 Research approach

Mesocosm experiments:

In order to assess the response of marine pelagic communities to artificial upwelling, one possibility is to carry out field experiments operating artificial upwelling structures. Such structures include artificial seamounts, electric pumps transporting brackish surface water into deeper water layers, or a bubble curtain produced by pipes installed on the (shallow) seafloor (Aure et al., 2007; Casareto et al., 2017; Handå et al., 2013; Jeong et al., 2013). Another approach would be nutrient enrichment experiments, whereby either DOW or nutrients (usually inorganic nitrogen (N) and phosphorus (P), often also silicon (Si)) are added to a body of water, preferably in micro- or mesocosms. One major advantage of these types of experiments, compared to the deployment of artificial upwelling structures, is that it creates an enclosed experimental environment with the possibility to control the parameters. When adding nutrients, N and P are usually added in a ratio in approximation to the canonical Redfield-ratio of N:P = 16:1 (Redfield, 1958). However, the signature, mode, and rate of nutrient supply can be adjusted to the research question. The cost-effectiveness is an advantage of the nutrient addition compared to DOW enrichment since the former is comparatively easy to conduct and less expensive than bringing up DOW for enrichment. Nutrient addition mimics artificial upwelling, as it enhances primary production (as e.g. shown by Gross et al., 1944; Schlüter, 1998; Vuorio et al., 2005). However, a replacement is not altogether realistic, since it for instance does not account for dilution, which occurs during real upwelling. Furthermore, DOW consists of more than the above mentioned macronutrients. It mostly consists of conservative ions like chloride and sulphate, but non-conservative constituents like calcium and bicarbonate, as well as some micronutrients (e.g. iron and zinc) and trace gases, have important impacts on the biology and the chemical and physical environment. Notwithstanding, the approach is feasible to simulate the biological stimulation in consequence of the upwelled and in most surface oceans bio-limiting macronutrients N, P, and Si.

Multiple nutrient enrichment experiments have been carried out looking at the responses of bacterial and phytoplankton communities (see e.g. Aksnes et al., 1985; Franz et al., 2012; Meyer et al., 2016; Sipura et al., 2005; Teira et al., 2011), others investigate the micro- and mesozooplankton (see e.g. Gismervik et al., 2002; Schlüter, 1998; Stibor et al., 2004; Svensen et al., 2002). However, to date there are few studies focusing on more than one trophic level and none that include responses of communities consisting of phytoplankton, micro- and mesozooplankton and fish to simulated artificial upwelling.

Motivation and expectations:

The applications of artificial upwelling are food supply for mariculture, carbon sequestration, and energy production. To create a system that facilitates the growth of small pelagic fish, such as Sardines and Anchovies, trophic chains with a low number of trophic levels and high trophic transfer efficiencies (Marten and Polovina, 1982) as well as a high nutrient utilisation efficiency (NUE) are required. To make the sequestration of atmospheric carbon feasible, high primary and export production must be assured (Platt and Sathyendranath, 1988). The amount of supplied nutrients is an important control variable for these parameters. The goal of this study is to identify which rate of nutrient addition results in high NUE, PP, and EE, and might thus be feasible to achieve efficient carbon export.

It is expected that nutrient addition stimulates phytoplankton growth, i.e. increasing net primary production. However, the increase of net community production (NCP) with nutrient addition has an upper limit: there is a point at which a pelagic system becomes limited by yet another factor apart from N, P, or Si limitation, e.g. environmental factors like light or CO_2 limitation, or biological ones, such as top-down control. These factors can prevent a further increase of primary production with nutrient addition. Beyond that point, NCP and NUE are expected to decrease compared to the system prior to limitation by another factor.

The higher the new production in a marine environment, the stronger the sinking flux of particulate organic carbon via the biological pump (Eppley and Peterson, 1979). Since new production is controlled by external nutrient input (Platt and Sathyendranath, 1988) the strength of the vertical OM flux is expected to increase with nutrient addition. Whether this relationship is a linear one is governed mainly by the strength of the export flux and the rate of microbial remineralization. It is expected that the export flux increases steeper than linearly with nutrient addition, owing to increased marine snow formation and faecal pellet production with increasing nutrient input. In this case, export efficiency may increase with increasing nutrient addition.

Scientific questions:

The objective of this study is to examine the effects of artificial upwelling on the export potential and nutrient utilisation of a pelagic system by conducting a nutrient-enrichment mesocosm experiment. The relationship between the rate of nutrient supply and the export efficiency as well as the efficiency of nutrient utilisation shall be investigated by examining the temporal developments in the N, P, and Si elemental pools.

The main scientific questions of the study are:

- What are the effects of simulated upwelling on the productivity of a pelagic system?

- How effective are nutrients utilised under different rates of nutrient addition?

- At what rate of nutrient addition are the added nutrients exported most efficiently in the form of biogenic matter?

In order to answer these questions, a four-week mesocosm experiment was conducted from August to October 2017 in Taliarte, Gran Canaria. In contrast to previous studies, this experiment allows for the investigation of the responses of the largest part of the pelagic community, including micro- and mesozooplankton as prey organisms for fish larvae, to the rate of simulated upwelling of deep water.

3 Materials and Methods

3.1 Experimental Setup

In September 2017, a four-week nutrient enrichment experiment in Taliarte on the east coast of Gran Canaria was conducted (Fig 3.1a). Eight mesocosms (M1 – M8) were filled with seawater and received daily additions of nutrients at different rates. The experiment consisted of four treatment levels, namely an un-treated control, a low, a medium and a high nutrient-treatment level, each treatment consisting of two mesocosms in themselves (see Fig 3.1b). Additionally, fish eggs just prior to hatching were added to one mesocosm of each treatment after two weeks of the experiment. Environmental parameters were measured daily in all mesocosms, water and sediment samples from the mesocosms were taken daily to determine biogeochemical and biological parameters, and two different nets for the collection of zooplankton were used regularly during the course of the experiment.

https://www.weltkarte.com/typo3temp/images/satellitenkarte-gran-canaria.jpg

Figure 3.1a: **Map of Gran Canaria** (left) **and Taliarte** on its East coast (right). Location of mesocosms is indicated by a yellow bar.

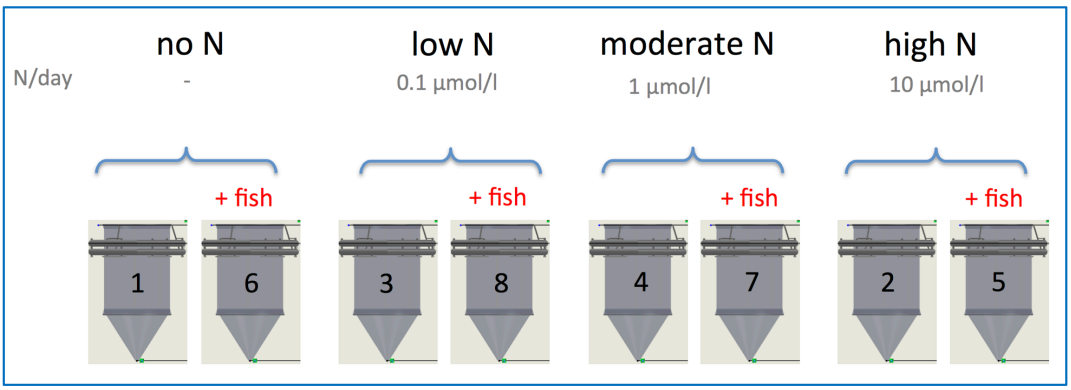


Figure 3.1b: **Different treatment levels** depicted by nitrate addition (N/day). Graph from Ulf Riebesell (2017).

The mesocosms used are basically smaller versions of the KOSMOS described in Riebesell et al. (2013), with a diameter of 2 m and ~4 m length. They consist of a cylindric mesocosm bag with a steel frame opening, weights at the lowest point to keep the bag vertically fully stretched, a sediment trap attached to the lower end of the bag, a flotation frame mounted to the bag opening and connecting all eight mesocosms in line, and plastic lids covering them. The funnel-shaped sediment trap is connected to a flexible hose at its lower end, which extends above the water surface. A wooden construction on the pier held beams equipped with winches reaching above each mesocosm, ensuring the centred veering and hoisting of measuring and sampling equipment.

The mesocosms were deployed at a pier located in the harbour of Taliarte in August 2017, and arranged randomly at the pier to avoid a possible location effect of the harbour. They were filled simultaneously on September 1st (t0) with seawater pumped from outside the harbour from around 10 m depth. The simultaneous filling of the mesocosms was achieved by the operation of a water flow partitioning device separating the water pumped from outside the harbour into eight pipes leading into the mesocosms. The water flow of each pipe was displayed by a flow rate counter, allowing for balancing the flows. On t0, 8200 L of water were filled into each mesocosm.

The inorganic nutrients nitrate (NO_3^- (N)), silicic acid ($Si(OH)_4$ (Si)), and phosphate (PO_4^{3-} (P)) were added to all but the control treatment in an overall ratio of Si:N:P = 8:16:1. The amount of nutrients added to the low, medium, and high treatment were 0.1, 1, and 10 μmol L^{-1} N; 0.05, 0.5, and 5 μmol L^{-1} Si; and 0.0063, 0.063, and 0.63 μmol L^{-1} P per day, with the low treatment receiving the lowest and the high treatment receiving the highest nutrient concentrations. The first nutrient addition (NA) was carried out on t4 between 7 - 8.30 pm. From then on, it was performed daily between 2 - 4 pm until t28 (see Fig 3.2). The Si addition started off with the same rate as N addition (Si:N = 1:1), but was suspended for three days

(t7, t8, and t9), and continued with half the original rate. This was done to reach an overall Si:N ratio of 1:2 for NA, which is more similar to the Si:N signature of the deep water masses of the region. Since the nutrients were contained in ultrapure water (Milli-Q water) for addition, enhancing the added volume of Milli-Q water (for the no, low, and medium treatments), or mixing it with NaCl (for the high treatment) enabled us to adjust the salinities of the mesocosms, counteracting the effects of evaporation, and the dilution due to high Milli-Q addition, respectively. Mesocosm volumes were calculated daily by adding the added-up NA volumes and subtracting the volumes taken out by sampling.

Beside nutrient addition, another treatment level was introduced to the mesocosms midway through the experiment in the form of fish eggs. On t14 the mesocosms M5, M6, M7, and M8 received "egg-cages" – a 8 L-plastic bottle with mesh-covered windows to assure for water exchange - containing 10,000 fish eggs of the Greater amberjack (*Seriola dumerili*). Thus, there was one fish larvae addition per treatment level in the second half of the experiment. The fish larvae were released into the mesocosms after hatching one day after introduction.

3.2 Sampling Procedure and Maintenance

The sampling schedule in Fig 3.2 depicts a timeline of the experiment with a chronological overview of the sampling and maintenance procedures.

On a daily basis, starting on t1, sampling of the sediment between 7 and 8.30 am and water column between 8 and 10 am took place until t30 and t29, respectively. We used submersible, 2 m long plastic tubes to take integrated 5 L samples from the water column. The daily water sample volume per mesocosm differed in a range of 10 - 45 L, depending on the volumes needed for certain parameters. From the integrated water samplers subsamples were directly transferred to 250 / 500 mL polypropylene bottles for dissolved organic matter and dissolved inorganic nutrients (dissolved inorganic nitrogen (DIN = nitrate (NO_3^-) + nitrite (NO_2^-) + ammonium (NH_4^+)), phosphorus (DIP = phosphate (PO_4^{3-})), and silica (DSi = $Si(OH)_4$)), total alkalinity (TA), and DMS/DMSP. These were handled with care, avoiding touching the bottle-openings to prevent contamination from fingerprints. They were stored in cool boxes until further processing. The remaining volume of the sampler was transferred to 10 L canisters, of which different quantities were used for filtration of biogenic silica (BSi), total particulate carbon (TPC), nitrogen (TPN), and phosphorus (TPP), as well as Chlorophyll *a* (Chl *a*) concentrations and for phytoplankton and microzooplankton composition and abundances. The canisters were stored in light-tight boxes after sampling. Sediments were sampled in 5 L Schott Duran glass bottles by means of a manually driven vacuum pump connected to the hose of the sediment trap

(~300 mbar pressure). Sediment samples were used for the content analysis of TPC, TPN, TPP and BSi. For sedimented zooplankton subsamples were taken every day from the regular sediment samples before further processing. Additionally, sediments were screened for fish larvae in the second half of the experiment after zooplankton subsamples had been taken from these. To avoid contamination, sampling was performed with nitrile gloves. All sample bottles and canisters were rinsed with MilliQ three times before every sampling day, and they were rinsed with sampled water just prior to sample collection.

Supplementing the water column and sediment sampling, CTD casts were performed daily between 9 - 11 am in each mesocosm, starting on t1. A CTD60M (Sea & Sun Technology) was used to provide profiles for temperature, salinity, density, pH, chlorophyll *a*, turbidity, oxygen, and PAR until t29.

For mesozooplankton samples vertical net hauls (Hydrobios Apstein net, 55 μm mesh size, ø 17 cm) of the upper 2.5 m of the water column were performed every second day, starting on t1. A bigger net to catch fish larvae (Hydrobios net, 500 μm mesh size, ø 50 cm) was used for the same depth range from t3 onwards approximately every four days. The last regular zooplankton sampling was performed on t29, the 30th of September. After the regular sediment, water column and mesozooplankton samples were taken, a ring net of the same diameter as the mesocosms was closed at the bottom of the mesocosm and hauled to the top, thus catching all surviving fish larvae (1,000 μm mesh size, 200 cm Ø) (for details see Sswat et al., 2018). To assure that all fish larvae were caught, this procedure was repeated once again in each mesocosm, directly after the first haul.

Furthermore, the mesocosms had to be maintained regularly in the course of the experiment. To prevent fouling, the mesocosm bags were cleaned both from the outside via diving and from the inside using a ring-shaped wiper (same diameter as mesocosm) with a weight at its bottom. The roofs were cleaned regularly as well. Cleaning of roofs and inside walls was performed every four days, roof cleaning starting on t3, inside cleaning on t4, cleaning of outside walls was performed every four to eight days, starting on t6.

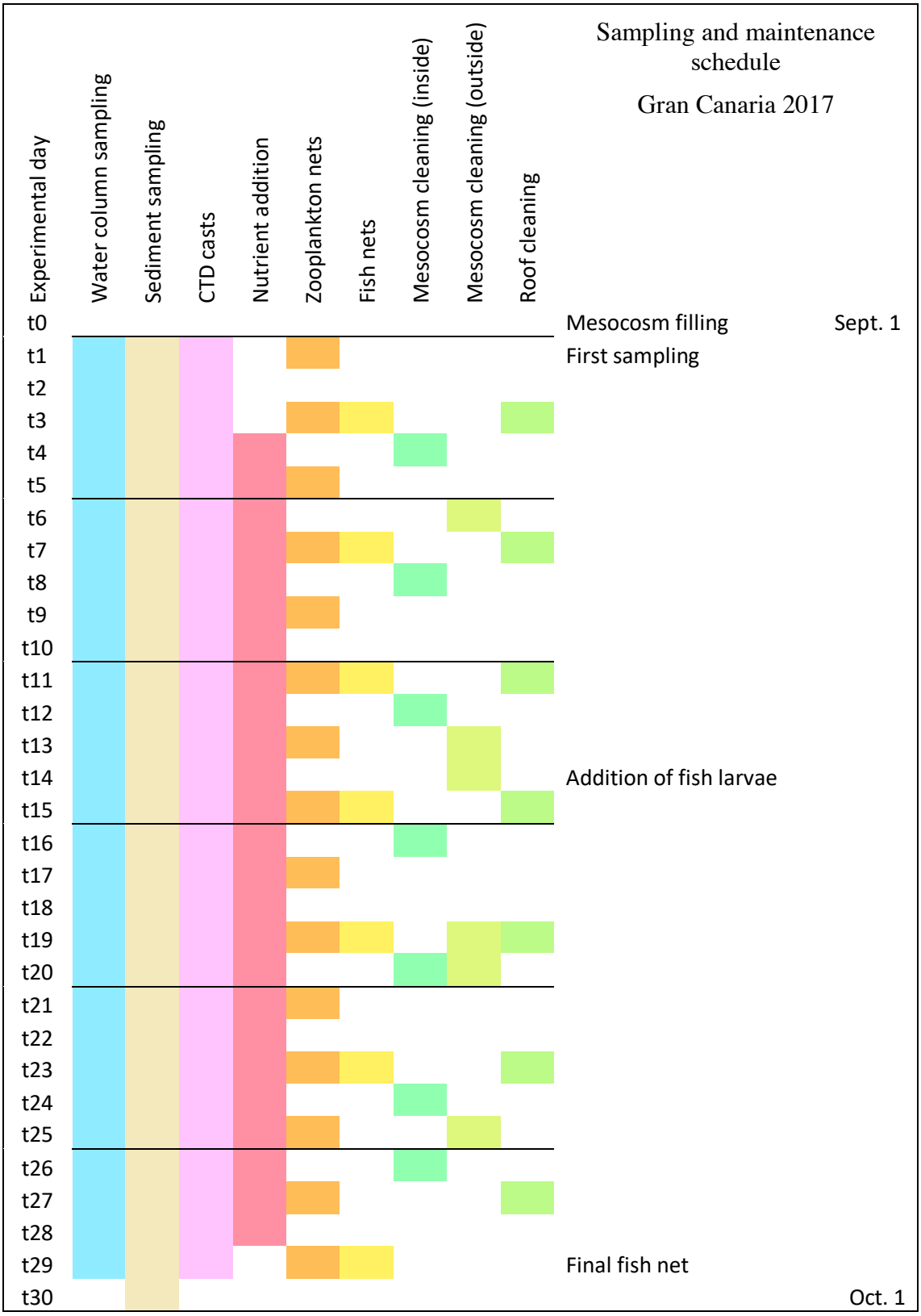


Fig 3.2: **Sampling and maintenance schedule**.

During and after the experiment, a wide range of environmental, biogeochemical, and biological parameters were measured. Which parameters were measured and how shall be described in the following.

3.3 Biogeochemical Parameters

To examine biogeochemical parameters like export fluxes, nutrient utilisation, or trophic transfer in response to artificial upwelling in pelagic communities, a broad range of analyses was performed. The sampling, the filtration and storage of samples, as well as the determination of nutrients was carried out according to Grasshoff et al. (2009).

3.3.1 Dissolved Inorganic Nutrients

Nitrate, nitrite, ammonium, phosphate, and silicic acid were measured via colorimetric analysis using a five channel Quaatro Autoanalyzer (Seal Analytic). Subsamples for inorganic nutrients were filtered through glass fibre filters (pore size 0.45 μm) in a clean environment and subsequently measured in the continuous flow analyser (CFA). The Quaatro Autoanalyzer moves the filtrate by means of a peristaltic pump, splits it into five different channels, and adds small nitrogen bubbles to separate the samples. Furthermore, it adds different colouring agents to each of the channels, depending on the nutrient to be measured. Every single channel leads to a spectrophotometer where the absorbance of the colouring compound is measured. The absorbance corresponds to the concentration of the respective nutrient.

Details on the measurements of the five compounds and their chemical detection, as well as information concerning the applied data processing and quality control was described by von der Esch (2017).

Note that the abbreviation for dissolved inorganic nutrients in this study is 'DIM', while the abbreviation 'DIN' is used for dissolved inorganic nitrogen.

Nitrate measurements on t2 were exceptionally high in M4 & M5 with 1.55 and 5.32 μmol/L nitrate, respectively. These were considered being outliers, as average nitrate concentrations before nutrient addition around t2 (t1, t3 and t4) were 0.05 and 0.06 μmol/L for M4 and M5, respectively.

3.3.2 Dissolved Organic Nutrients

Dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) samples were taken every second day. They were filtered through combusted glass fibre filters (Whatman GF/F, pore size 0.75 μm) using gentle vacuum filtration (<200 mbar) and stored at -20 °C until

the end of the experiment. Prior to measurements, they were autoclaved for 30 min in the oxidizing solution Oxisolv (Merck) to decompose organic material. Subsequent measurements of nitrate and phosphate in the Quaatro Autoanalyzer resulted in total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) concentrations. DON and DOP were obtained by subtracting the dissolved inorganic nitrogen and phosphorus from the total dissolved concentrations.

The limit of detection (LOD) for dissolved nutrient measurements (both for dissolved inorganic nutrients and DOM) was calculated according to IUPAC standards and is defined as the smallest measurable concentration with a signal that is significantly higher than the one of the reagents concentration in the blank (Thompson and Wood, 1995). LODs were calculated for each measurement day, and, as they were consistent throughout the experiment, mean LODs were calculated for each of the measured dissolved inorganic and dissolved organic nutrients.

3.3.3 Particulate Matter and Chl *a*

Water column:

Particulate matter (PM) from the water column was collected on filters using gentle vacuum filtration (≤ 200 mbar). Pre-combusted glass fibre filters (0.7 μm pore size, Whatman) were used for TPC, TPN, and TPP and cellulose acetate filters (0.65 μm, Whatman) for BSi. Since the particulate inorganic carbon (PIC) content of our samples was assumed to be low, TPC filters were exposed to fuming hydrochloric acid to remove PIC. TPC and TPN filters were stored in pre-combusted glass petri dishes and dried over night at 60 °C. The next morning, these petri dishes were packed in tin foil and stored at -20 °C until analysis, which was performed after the experiment had ended. They were analysed by gas chromatography according to Sharp (1974) on an acetanilide (C_8H_9NO) and soil standard (Hekatech) calibrated CN analyser (Euro EA-CN, Hekatech). Since particulate inorganic phosphorus (PIP) was expected not to be abundant, we restrained from the laborious splitting of PIP from POP, and used TPP as a proxy for POP instead. TPP filters were cooked with Oxisolv (Merck) to oxidize the organic phosphorus to orthophosphate (as for DON, DOP, see Sect. 3.3.2), and the remaining inorganic phosphate was measured spectrophotometrically according to Hansen and Koroleff (2009). The cellulose acetate filters for BSi were kept in plastic petri dishes and stored at -20 °C. They were leached with sodium hydroxide at 85 °C for 135 min, to convert BSi to DSi, which was then measured spectrophotometrically, as well according to Hansen and Koroleff (2009). Measurement of TPP and BSi was carried out simultaneously between one and three days after the sampling.

Chl *a* was filtered on glass fibre filters like TPC, TPN and TPP. Samples were kept cool and dark at all times, to prevent photo oxidation of pigments. The filters were then frozen overnight at -20 °C, and pigment content was determined fluorometrically according to Welschmeyer (1994). Pigments were extracted using 90 % aqueous acetone and their absorption was measured using a fluorometer directly afterwards. From that, Chl *a* concentrations were calculated.

Sediments:

To estimate the elemental composition of PM in the sediments, the sediment bottles were gently shaken and subsamples were taken afterwards using plastic pipettes (between 1 and 30 mL). Subsamples for TPC, TPN, TPP, and BSi were filtered and measured the same way as PM samples of the water column. Summed up PM contents of the sediments were divided by the calculated mesocosm volumes (see Sect. 3.1) to receive concentrations in μmol/L for the respective compounds.

Mesozooplankton that ended up in the sediments was not removed before PM filtration, and is thus accounted for in the sediment flux. Fish larvae, however, were searched for and removed from the sediments from t14 on, and thus do not contribute to the vertical flux.

The TPC and TPN sediment contents of the following days could not be measured: M1, M2, M3, M4 & M5 on t5, M4 on t23, M3 & M8 on t25, and M6 on t29. Values were therefore estimated by linear interpolation.

3.4 Environmental Parameters

The environmental parameters measured during the experiment were oxygen, salinity, temperature, pH, and total alkalinity (TA). Oxygen, salinity, temperature, and pH were measured using a CTD probe equipped with the respective sensors, providing daily depth profiles from the surface to close to the bottom of the mesocosms. Samples for TA were taken every second day and processed directly. They were measured by automated potentiometric titration using an 862 Compact Titrosampler (Metrohm) following Grasshoff et al. (2009).

From TA and pH, dissolved inorganic carbon (DIC) and pCO_2 were calculated using the MS Excel program CO2SYS, Version 01.05, by Pierrot et al. (2006). The carbonate dissociation constants (K1 and K2) from Mehrbach et al. (1973), refit by Dickson and Millero (1987), were used, and input data included temperature and salinity.

3.5 Biological Parameters

To determine the phytoplankton and microzooplankton composition and abundances, subsamples were taken from the 10 L canisters, concentrated, counted, and identified under the microscope using the Utermöhl-method (Utermöhl, 1958). Counting chambers were used to calculate cell numbers, cell volumes, and biomass of species.

Abundances for mesozooplankton from both the water column and the sediments were estimated by counting organisms with a stereomicroscope. Species composition was determined from abundance data for the size classes 55-200, 200-500, 500-780, and >780 μm.

Fish larvae found in the fish nets and in the sediments were used to calculate fish larvae survival. After the last regular sampling day, the final ring net was used to catch the remaining larvae. However, only one of the added larvae survived until the end of the experiment (unpublished data, Michael Sswat). Therefore, the impact of the fish larvae is considered to be very low to non-existent.

3.6 Data Analysis

3.6.1 Nutrient Budgeting

To assess the effects of simulated artificial upwelling on a pelagic ecosystem, we describe the elemental pools of the bio-limiting elements N, P, and Si and calculate their mass balances for the conducted mesocosm study. Note that an 'elemental pool' of a nutrient in this study is regarded as the nutrient's 'biologically active pool'. Hence, the N elemental pool does not include nitrogen gas.

The temporal development of N, P, and Si pools can be displayed by nutrient budgeting for each of the three macronutrients. These budgets comprise the net community production (NCP) on the one side, and the sum of taken up dissolved inorganic nutrients (ΔDIM) on the other. If all elemental pools of N, P, and Si are assessed and the measurements are accurate, the NCP and ΔDIM should be equally high, and the budget should close.

NCP was calculated following Hansell and Carlson (1998). They state that one way to derive NCP is via the net biological drawdown of carbon dioxide or other essential nutrients like nitrate. Alternatively, it can be calculated by the accumulation of organic products, i.e. the increases of DOM and PM in the water column plus the amount of vertically exported PM. This is shown for the N elemental pool in equation 2 (the N pool will be used exemplarily for all following parameters).

$$NCP_N = \Delta PON_{susp} + \Delta DON + \sum PON_{sed} \quad (2)$$

Using this equation, the rate of NCP can be estimated when the time interval is specified. However, since we encountered severe problems estimating DON and DOP, we refrained from using DOM data for NCP calculations. This will be discussed thoroughly in chapter 5 (Sect. 5.2.1). Since there is also no form of (dissolved) organic silicon, NCP is only composed of ΔPM_{susp} and $\sum PM_{sed}$ for all three elements in this study.

Daily changes in the inorganic nutrient pools were calculated for the experimental day t(x) as seen for DIN in Eq. 3:

$$\Delta DIN_{t(x)} = DIN_{t(x)} - (DIN_{t(x-1)} + NA_{t(x-1)}) \quad (3)$$

These daily changes in DIM were added up for each nutrient pool to receive accumulated DIN, DIP, and DSi changes (ΔDIM). ΔDIM was first calculated on t5 by subtracting the averaged starting conditions (DIM between t1 and t4) from DIM_{t5}. Net changes for ΔPM_{susp}

(ΔPON_{susp}, ΔPOP_{susp}, and ΔBSi_{susp})and ΔDOM were calculated as well by subtracting the starting conditions of the respective parameter from the concentration of each measurement day.

3.6.2 Utilisation of nutrients

To assess which part of the nutrient addition was being taken up by the communities in the different treatments, we calculated the nutrient utilisation efficiency (NUE) (Eq. 4). This is described as the ratio between the taken-up DIM and the summed-up NA plus the DIM starting condition.

$$NUE_N = \frac{\Delta DIN}{\sum NA + starting\ condition} \quad (4)$$

A hypothetical NUE_N of 1 would mean that all added nitrate is at some point taken up and/or incorporated in OM, while a NUE_N of 0.5 would mean that half of all added nitrate is taken up.

3.6.3 Export parameters

To determine which part of the NCP sank out of the mesocosms, we estimated the export potential (EP) (Eq. 5). This is described by the ratio between the sum of sedimented PM to the sum of NCP. EP will be calculated for all four treatment levels.

$$EP_N = \frac{\sum PON_{sed}}{\sum NCP} \quad (5)$$

EP is in this study the equivalent to export efficiency. There are two differences between the two. Firstly, NCP is used for the calculation of EP, while PP is used in the e-ratio. Secondly, EE is defined for the base of the euphotic zone, while EP is calculated for only a couple of meters depth, i.e. the length of our mesocosms.

Since all calculated parameters (NCP, NUE, EP) are dependent on the starting conditions of either DIM, sedimented PM, or suspended PM, they were first calculated for t5, i.e. the first day of nutrient addition. Therefore, also the PM_{sed} data from t1 - t4 was not included in the parameters NCP and EP. The nutrient budgets start with the PM_{sed} data from t5 as well.

Furthermore, NUE was only calculated for the treatments receiving nutrient addition (low, medium, and high).

3.6.4 Statistics

A one-way ANOVA was performed to test for differences in the starting conditions (t1 - t4) of dissolved inorganic nutrients and particulate suspended matter between the four different nutrient addition treatments (see Table 4.1). This was done using the *R* software (R Core Team, 2015). During data analysis it became apparent that a nutrient addition effect

can clearly be seen in our data, which is why no further statistical analyses were carried out in this study.

4 Results

Based on the development of Chl *a* and DIM measurements, the experiment was divided into three distinct phases. Phase I (t1 - t4) is to be seen as the starting condition, i.e. the clear-water phase. Phase II (t5 - t11) is the bloom phase, and starts with the first nutrient addition. Phase III (t12 - t30), the post-bloom phase, starts when most mesocosms have reached their blooming peak. This is not the case for the medium treatment, where the bloom phase lasted longer (Fig. 4.1.2). For comparability however, experimental phases are applied equally to all treatments.

The starting conditions of our mesocosms did not differ significantly between treatments regarding any of the dissolved inorganic nutrients and the suspended particulate matter (Table 4.1).

		control	low	medium	high	ANOVA	
		µmol/L ± SD				test statistic	p-value
DIN	DIN	0.68 ± 0.50	0.73 ± 0.25	0.61 ± 0.24	0.63 ± 0.17	0.22	0.885
	DIP	0.057 ± 0.015	0.069 ± 0.011	0.069 ± 0.010	0.070 ± 0.011	2.2	0.105
	DSi	0.84 ± 0.11	0.82 ± 0.10	0.83 ± 0.13	0.82 ± 0.09	0.07	0.978
PM	PON	1.3 ± 0.26	1.3 ± 0.20	1.3 ± 0.14	1.2 ± 0.20	0.16	0.926
	POP	0.080 ± 0.032	0.066 ± 0.016	0.090 ± 0.071	0.065 ± 0.023	0.67	0.579
	BSi	0.25 ± 0.077	0.28 ± 0.034	0.25 ± 0.039	0.25 ± 0.065	0.64	0.596

Table 4.1: **Starting conditions of mean DIM and suspended PM concentrations** for the four different NA treatments (time period: t1 - t4) in μmol/L ± standard deviation (SD). F-values (test statistic) and p-values of the carried out one-way ANOVA are shown for each parameter (significance level: $p \leq 0.05$). Note that DIN values for M4 and M5 on t2 were not included here.

4.1 Dissolved inorganic nutrients and chlorophyll *a*

The dissolved inorganic nutrient concentrations measured were very similar within treatment levels, but display great differences between them (Fig 4.1.1). The highest NO_3^- + NO_2^- values in the high treatment, for example, were two orders of magnitude higher than the highest ones in the medium treatment. In the high treatment, there was a nutrient peak during the bloom phase around t8, followed by a minimum around t12, and again a subsequent increase until the end. There was an initial peak in the medium treatment as well, after which nutrients were more or less fully taken up every day. In the low treatment level, there was silicic acid and phosphate when starting the experiment, but concentrations decreased towards the end, while nitrate plus nitrite concentrations remained low throughout the experiment. In the control mesocosms, dissolved inorganic nutrient concentrations were low at all times.

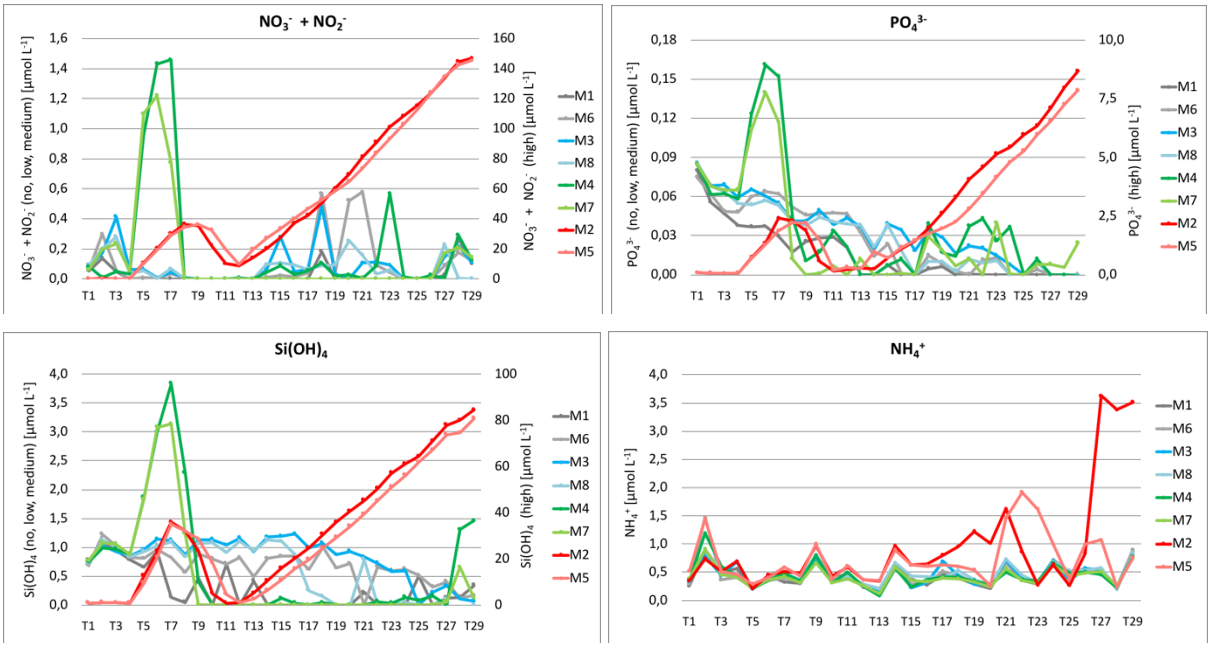


Figure 4.1.1: **Inorganic nutrient concentrations during the course of the study**. Shown are nitrate and nitrite (top left), phosphate (top right), silicate (bottom left), and ammonium (bottom right) concentrations in each mesocosm. Note the different y-axes for the high treatment for nitrate and nitrite, phosphate, and silicate. The colour code is: red for high, green for medium, blue for low, and grey for control treatment mesocosms. This colour code will be used throughout this study.

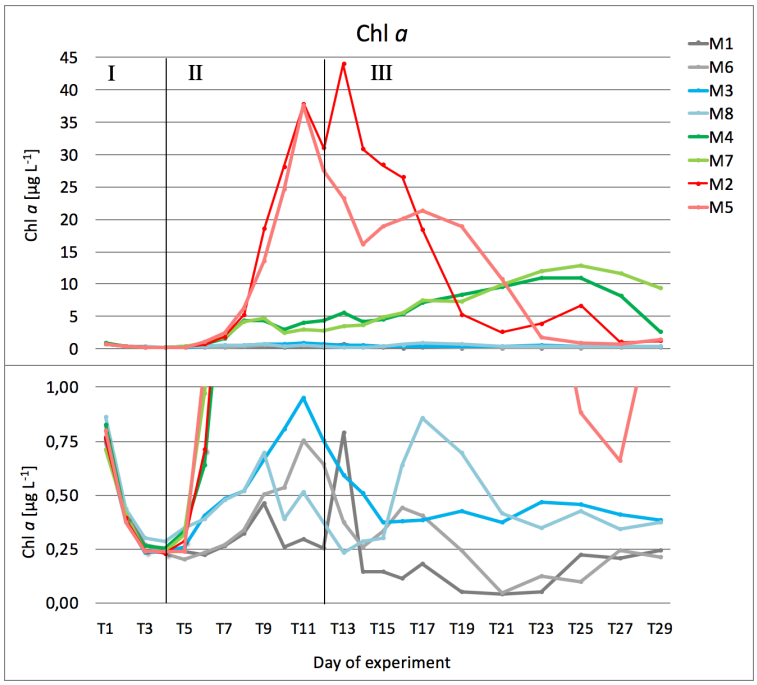


Figure 4.1.2: **Chlorophyll a concentrations over time** in each mesocosm. The bottom graph shows the lower treatments in higher resolution. Roman letters denote experimental phases.

Starting with phase II, Chl *a* concentrations were clearly different between treatments (Fig 4.1.2). An increase of Chl *a* after the first nutrient addition (t4) can be seen in all treatments, even in the control without nutrient addition. The increase was fastest in the medium and high

treatments and highest in the high treatment, where it reached values of up to 40 μg/L. After phase II, values decreased gradually in the high treatment until the end of the experiment. In the medium treatment, chlorophyll was built up until t25 and decreased thereafter. The no and low nutrient treatments displayed values of more than one order of magnitude lower than the other treatments and reached a peak around t10. The values in the control scenario were slightly lower than in the low treatment.

4.2 Carbonate chemistry

During nutrient addition, all but the control treatment underwent changes in their carbonate chemistry. Figure 4.2 shows temporal changes in pCO_2 in all mesocosms. There was a strong decrease during phase II in both the medium and high treatment, though the rate of this decrease was faster in the high treatment than it was in the medium treatment. The former dropped to pCO_2 values of 14.2 and 12.8 μatm in M2 and M5 on t19, respectively, the latter to values of 40.6 and 33.6 μatm in M4 and M7 on t27, respectively. The control treatment showed no pronounced changes while the low treatment experienced a slight decrease in CO_2 partial pressure.

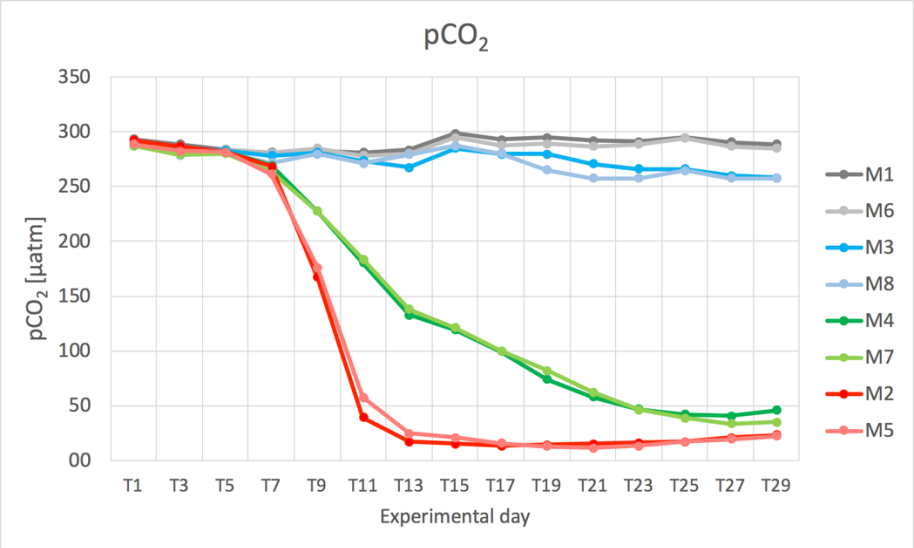


Figure 4.2: **Development of CO_2 partial pressure in the course of the experiment** in each mesocosm.

4.3 Temporal development in elemental pools

4.3.1 Nitrogen

Figure 4.3.1 describes the mass balance for the elemental nitrogen pool in all four treatment levels (a-d). In theory, net community production should equal the sum of consumed dissolved inorganic nutrients. However, all mass balances showed more or less pronounced discrepancies. Table 4.3.1 shows the discrepancies between NCP and ΔDIM for all treatment levels and nutrients during phase III.

In the control treatment, NCP_N was higher than ΔDIN at all times. There was a considerable accumulation of sedimented PON over time, whereas there was no corresponding decrease in any of the other pools. Similar to the control treatment, NCP_N in the low treatment was higher than ΔDIN. However, the discrepancy was lower than in the control. In the medium treatment on the other hand, ΔDIN was higher than NCP_N. In there, suspended PM comprised a larger part of NCP_N than sedimented PM. In all other treatments sedimented PM made up the major part of the production. In the high treatment, ΔDIN was a lot higher than NCP_N during phase III. The suspended PM was high during and at the end of phase II, and decreased subsequently until the end of the experiment, which correlated with an increase in sedimented PM.

Mass balance discrepancies in phase III

	control	low	medium	high
N	68.6%	19.3%	-29.3%	-56.1%
P	185.3%	11.2%	-46.5%	-62.6%
Si	-78.4%	35.0%	-0.9%	-32.5%

Table 4.3.1: **Discrepancies between NCP and ΔDIM** in the N, P, and Si mass balances during phase III**.** Discrepancies are shown in % for the four nutrient addition treatments. Positive discrepancies occur when NCP > ΔDIM (NCP is x % higher than ΔDIM). Negative discrepancies occur when NCP < ΔDIM.

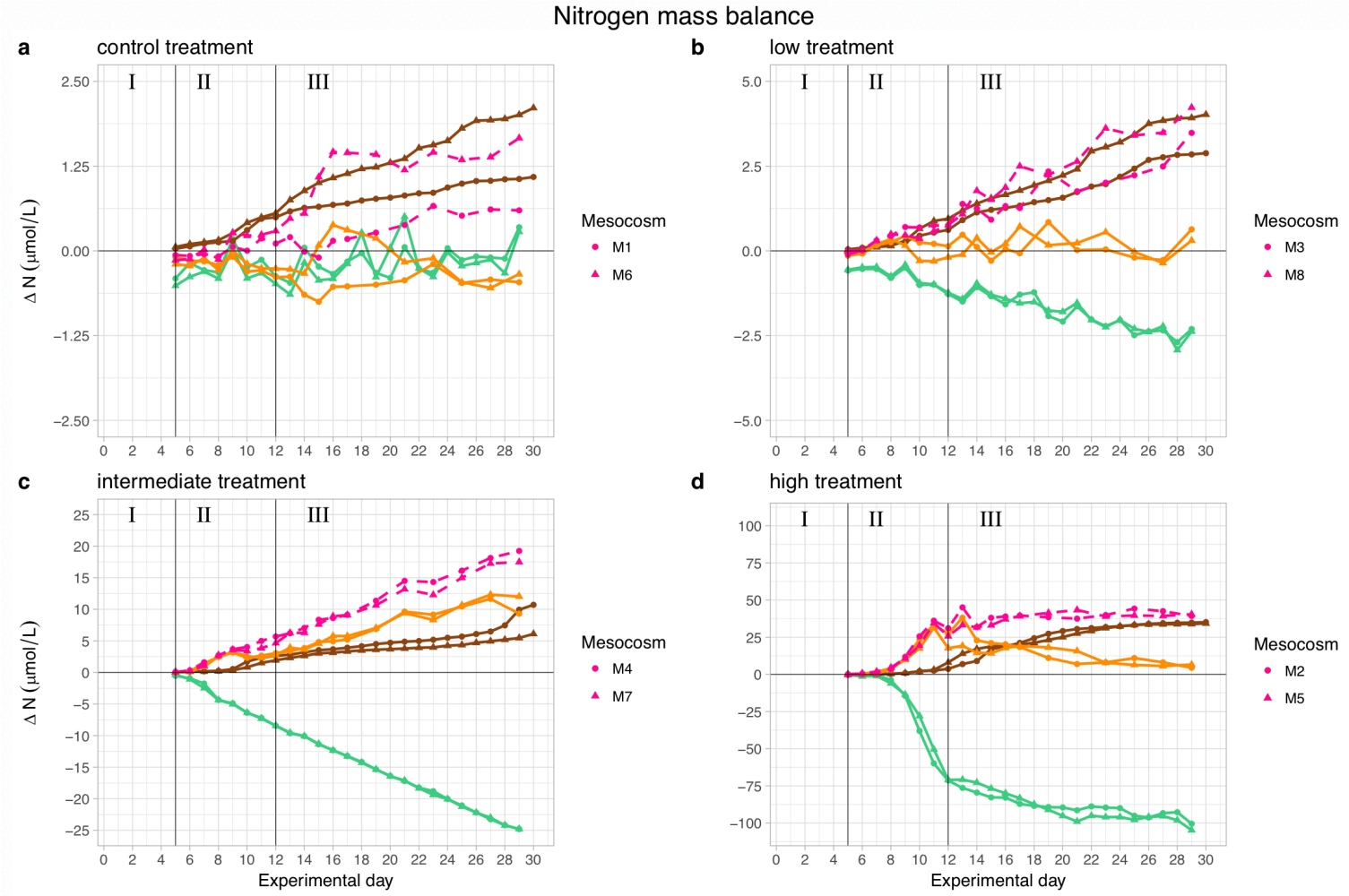


Figure 4.3.1: **Temporal development of nitrogen pools**. Displayed are ΔDIN (light green), sedimented PON (brown), ΔPON_{susp} (orange), and NCP_N (pink). Roman letters denote experimental phases. Temporal resolution of data is daily for ΔDIN and PON_{sed}, and one to two days for ΔPON_{susp} and NCP_N.
(**a**) control, (**b**) low, (**c**) medium, (**d**) high treatment

4.3.2 Phosphorus

Similar to N, the P budgets did not fully close in any of the mesocosms. In the control treatment, the consumed inorganic nutrients were much lower than NCP_P (see Table 4.3.1). There were three data points of comparatively high POP_{susp}, which strongly elevated NCP_P, but they were not mirrored in POP_{sed} or ΔDIP (Fig 4.3.2). In the low treatment NCP_P was higher than ΔDIP as well, but the overall discrepancy was lowest in this treatment (-0.4 % in M3, and +22.7 % in M8 in phase III). The high within treatment difference is due to higher sedimented POP values in M8. There was an increase in sedimented POP in both mesocosms in the second half of phase III which was not reflected in any of the other P pools. In the medium treatment ΔDIP was higher than NCP_P. In the high treatment the same trend was visible, though more distinct: here, ΔDIP was almost three times higher than NCP_P during phase III (-62.6 %). The over- and underestimations in the P budgets are consistent with those of the N budgets.

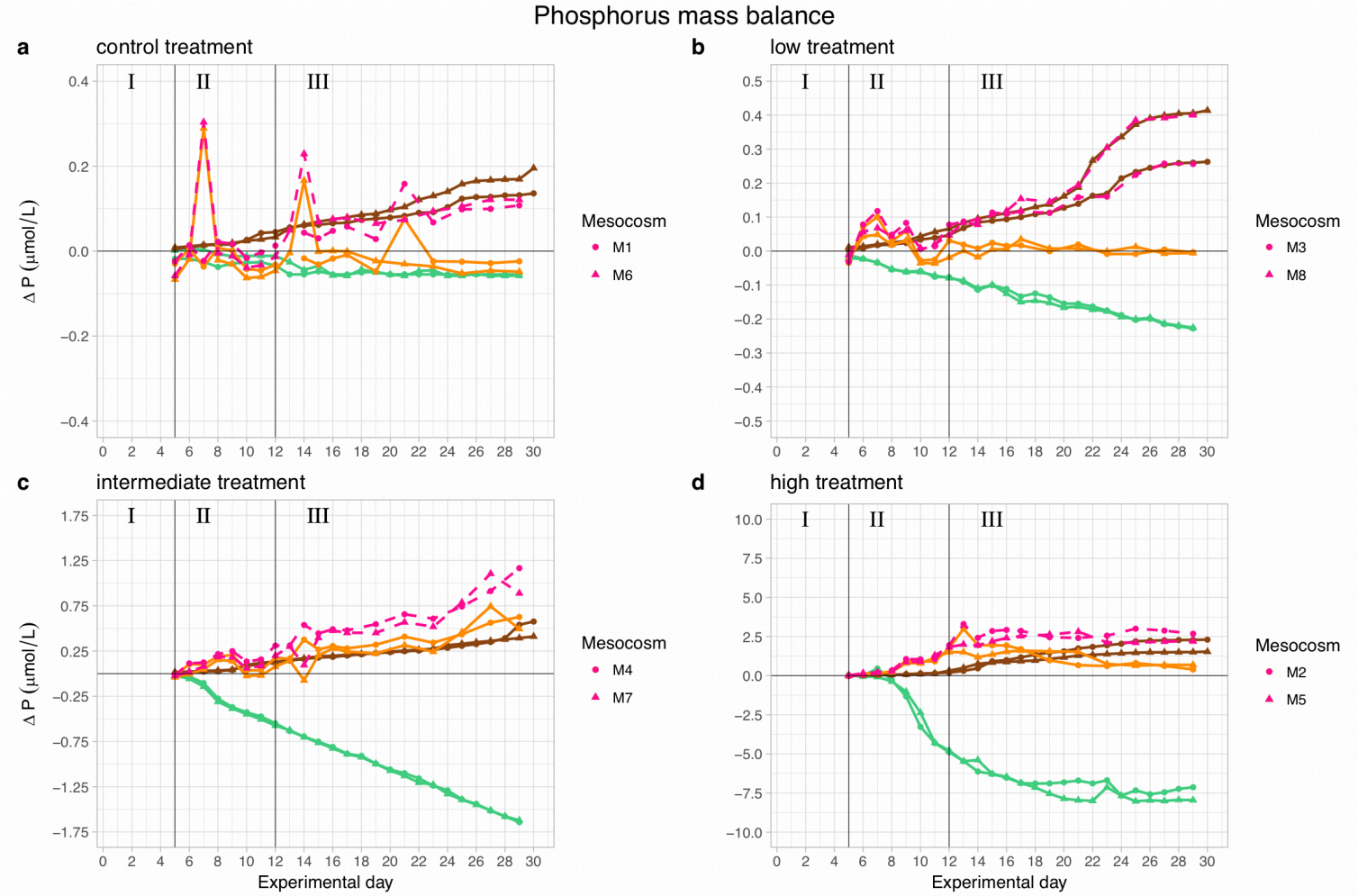


Figure 4.3.2: **Temporal development of phosphorus pools**. Displayed are ΔDIP (light green), sedimented POP (brown), ΔPOP_{susp} (orange), and NCP_P (pink). Roman letters denote experimental phases. Temporal resolution of data is daily for ΔDIP and POP_{sed}, and one to two days for ΔPOP_{susp} and NCP_P.
(**a**) control, (**b**) low, (**c**) medium, (**d**) high treatment

4.3.3 Silicon

In the Si control treatment, there was a steady accumulation of sedimented BSi, and an increase of NCP_{Si} over time. Although we found an increase in consumed DSi, there is strong variation in the data which is not mirrored in any other pool. At the very end, NCP_{Si} was lower than ΔDSi, and the budget did not close (-78.4 % mean discrepancy in phase III, see Table 4.3.1). There is one BSi_{susp} outlier which is not mirrored in PM_{sed} or ΔDSi. The low treatment was characterised by a slow increase of BSi_{sed} and ΔDSi until t15, and a higher increase of both parameters thereafter, coupled with an increase in suspended BSi. The mean discrepancy between NCP_{Si} and ΔDSi in phase III in the low treatment was +35.0 %. However, this is mainly driven by the differences between NCP and ΔDIM at the beginning of phase III. Discrepancies become lower towards the end of the experiment, e.g. +0.6 % and 11.2 % in M3 and M8 on t29, respectively. The Si budget in the medium treatment was virtually closed, with a mean discrepancy between NCP_{Si} and ΔDSi during phase III of -0.9 %. At the end of phase III, BSi_{susp} in M4 decreased while BSi_{sed} increased. The same trend can be seen in the N and P budgets but it was most pronounced for Si. In the high treatment, ΔDSi was about 1.5 times higher than NCP_{Si} in phase III. Noticeable is the contrast of a very high DSi uptake during phase II compared to almost no Si uptake during phase III (see Fig 4.3.3). Except for the control treatment, the over- and underestimations in the Si budgets are consistent with those of the N and P budgets.

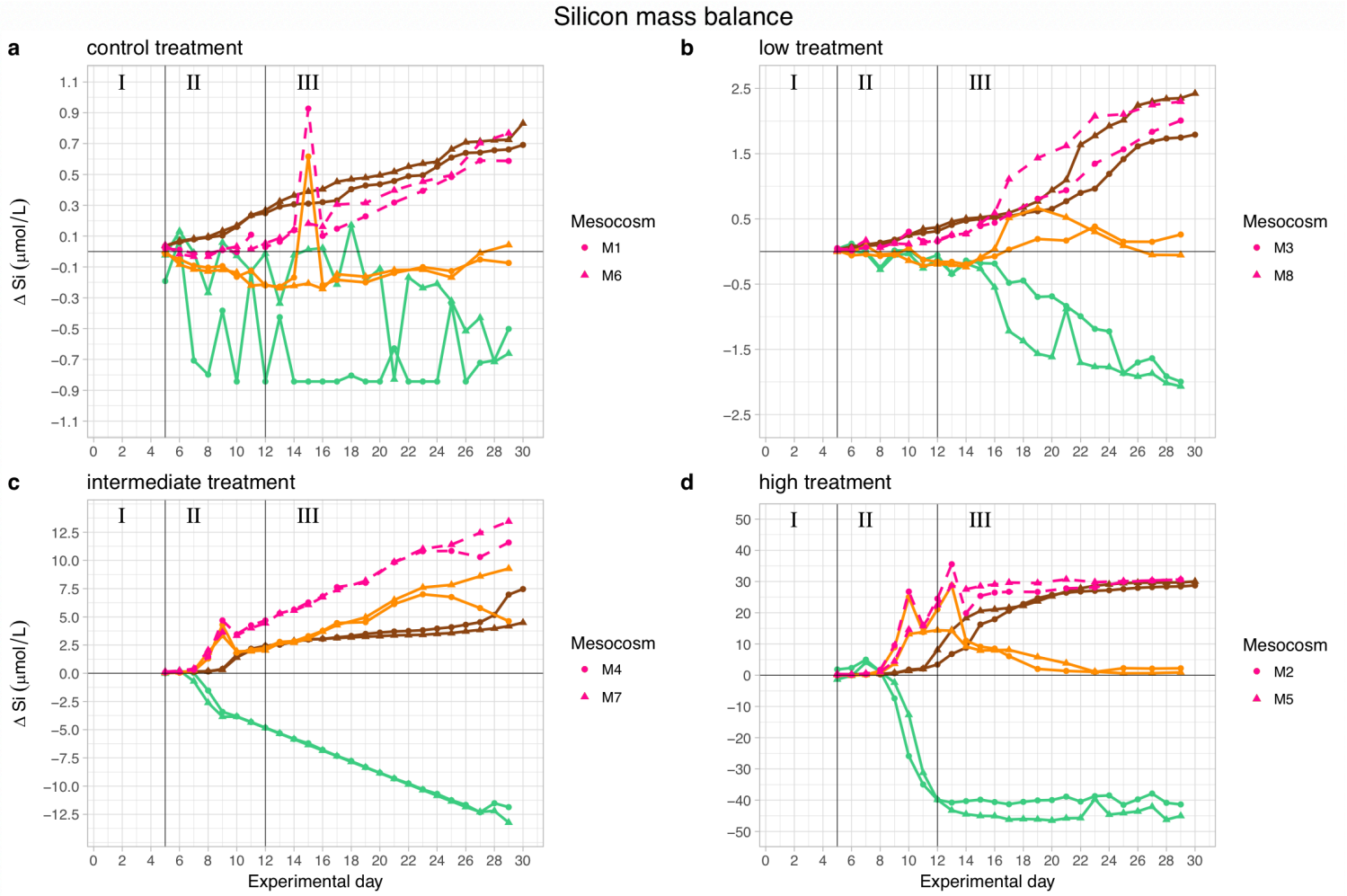


Figure 4.3.3: **Temporal development of silicon pools**. Displayed are ΔDSi (light green), BSi_{sed} (brown), ΔBSi_{susp} (orange), and NCP_{Si} (pink). Roman letters denote experimental phases. Temporal resolution of data is daily for ΔDSi and BSi_{sed}, and one to two days for ΔBSi_{susp} and NCP_{Si}.
(**a**) control, (**b**) low, (**c**) medium, (**d**) high treatment

4.4 Net community production

Figure 4.4 shows NCP in phases II & III as a function of nutrient addition for each treatment and nutrient. The general trend was an increasing NCP with increasing NA. Notwithstanding, the quantitative difference between the control and low treatment was often minor, especially for NCP_{Si} and NCP_{N}. There was only a small quantitative difference between the medium and the high treatment in phase II, whereas it was more distinct in phase III. Even in the latter phase though, the data suggests that NCP did not increase linearly with nutrient addition.

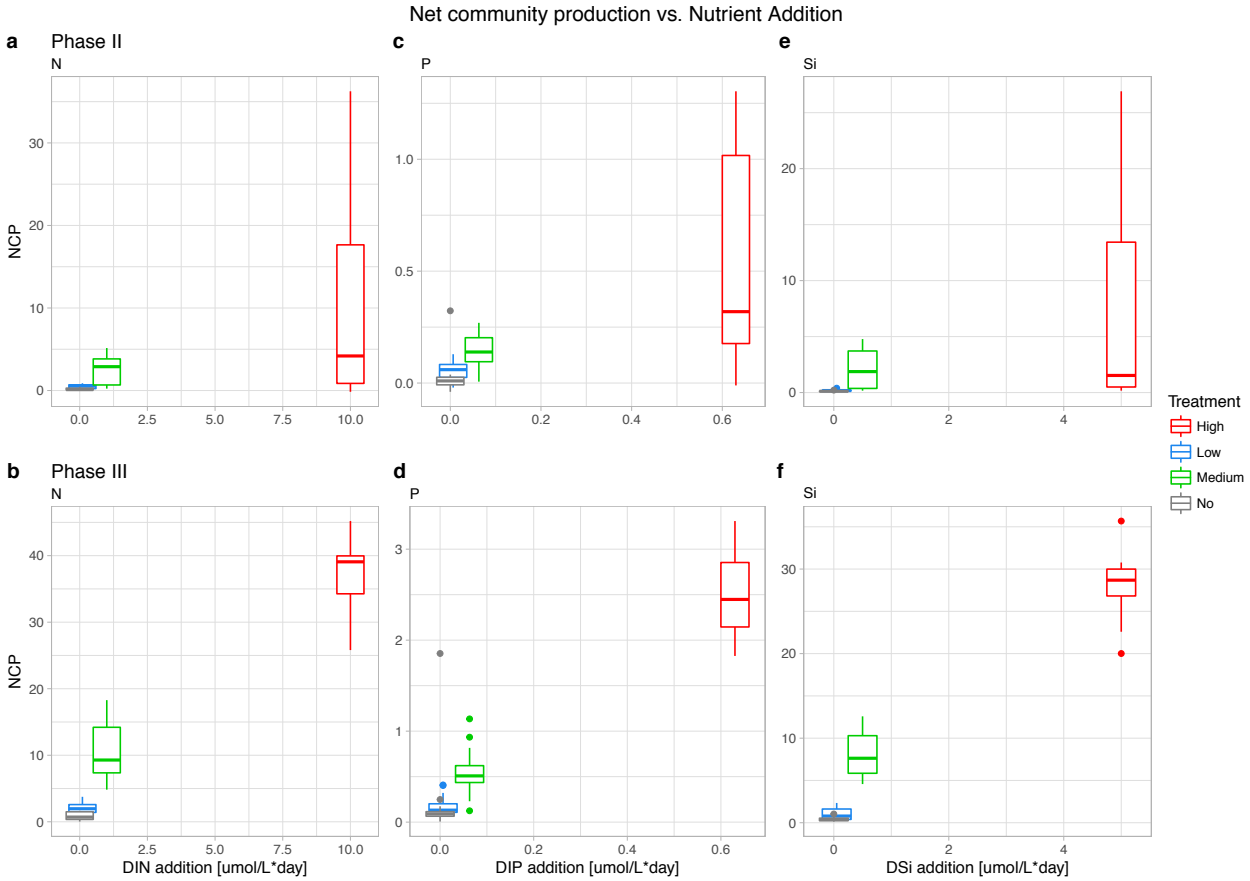


Figure 4.4: **Net community production vs. nutrient addition**. Boxplots depict NCP integrated over phase II (upper plots), and phase III (lower plots) for the N, P, and Si pools. They contain NCP data of all mesocosms (pooled as the four NA treatment levels) for all days of phases II & III. The whiskers denote the lowest NCP value still within 1.5 times the interquartile range (IQR) of the lower quartile, and the highest NCP value still within 1.5 times the IQR of the upper quartile. Daily DIN, DIP, and DSi additions in μmol/L/day are displayed on the x-axis.
(**a** + **b**) nitrogen, (**c** + **d**) phosphorus, (**e** + **f**) silicon

4.5 Nutrient utilisation efficiency

The study showed that artificially added nutrients were taken up most efficiently in the medium treatment (Fig 4.5). In this treatment, NUE rose steeply and quickly after the first

nutrient addition and remained high thereafter. The high treatment started rising later than the medium treatment, though just as steeply. It peaked in a high NUE between phases II and III, and decreased thereafter. The peak was highest, and the increase steepest for NUE_{Si}. The decrease was strongest for NUE_N and NUE_{Si} (mean NUE_{t29}: 0.41 and 0.34, respectively) whereas P was still taken up at a higher rate at the end of phase III (mean NUE_{t29}: 0.48). The low treatment became more efficient over time for all nutrients. Whereas P was the first nutrient to be utilised very efficiently, Si was second in line, though it took longer to get there. N, although being utilised most efficiently at the beginning (mean $NUE_{phase\ II}$: 0.60), did not get to a point where all added N was taken up.

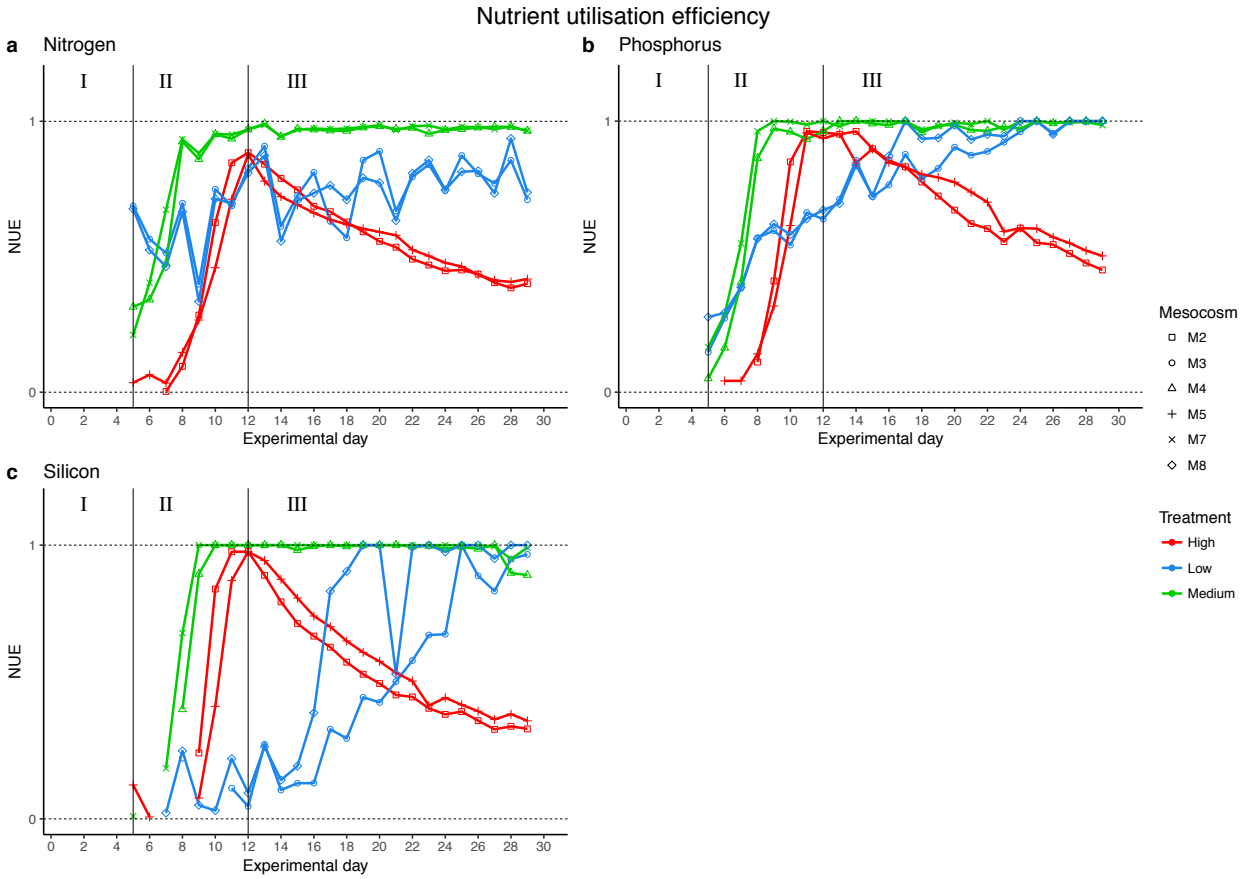


Figure 4.5: **Temporal development of nutrient utilisation efficiency**. The figure shows each mesocosm of the low, medium, and high treatment. Roman letters denote experimental phases.
(**a**) nitrogen, (**b**) phosphorus, (**c**) silicon

4.6 Export potential

The temporal development of EP is depicted in Fig 4.6a. The high treatment level had a low export potential in phase II, followed by an increase throughout phase III which can be seen in all three nutrient budgets. The fraction of NCP which was exported in the medium

treatment was lower than in the high treatment. However, there was an increase around t28 in the medium treatment mesocosm M4. Furthermore, an EP minimum in the two highest treatments during phase II is followed by a subsequent increase, which starts later in the high than in the medium treatment. The low treatment was characterised by a high export potential, and, especially in the N and P pools, values > 1. The same was the case in the control treatment with even more values > 1.

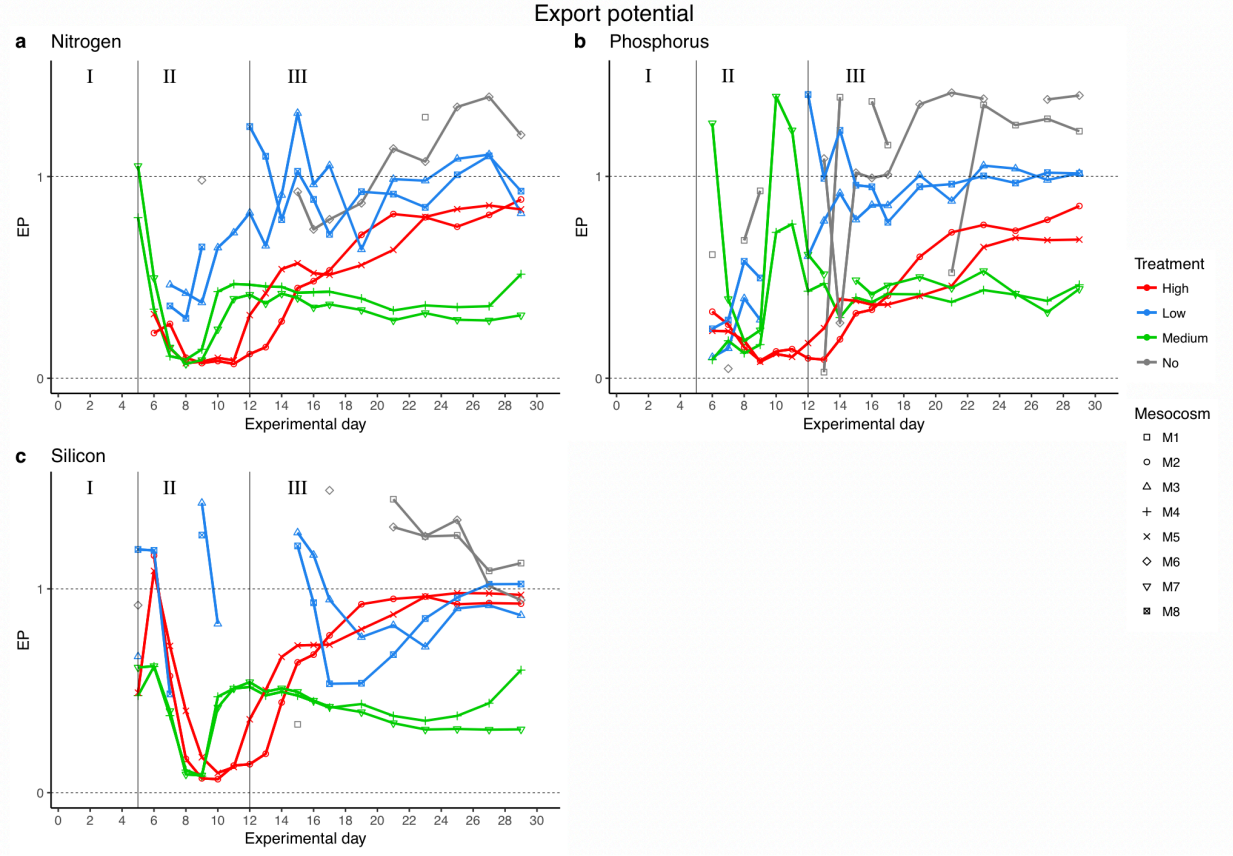


Figure 4.6a: **Temporal development of export potential**. The figure shows each mesocosm of the control, low, medium, and high treatment. Roman letters denote experimental phases.
(**a**) nitrogen, (**b**) phosphorus, (**c**) silicon

For better visualization, export potential is displayed as a function of nutrient addition, integrated over phases II and III, in Fig 4.6b. This shows that additionally to the values > 1 there were also EP_P values < 0 in the low and in the control treatment. Nevertheless, the low treatment was clearly more efficient in exporting biogenic material to the sediment trap than the two higher treatments. Export potential did thus not increase with nutrient addition.

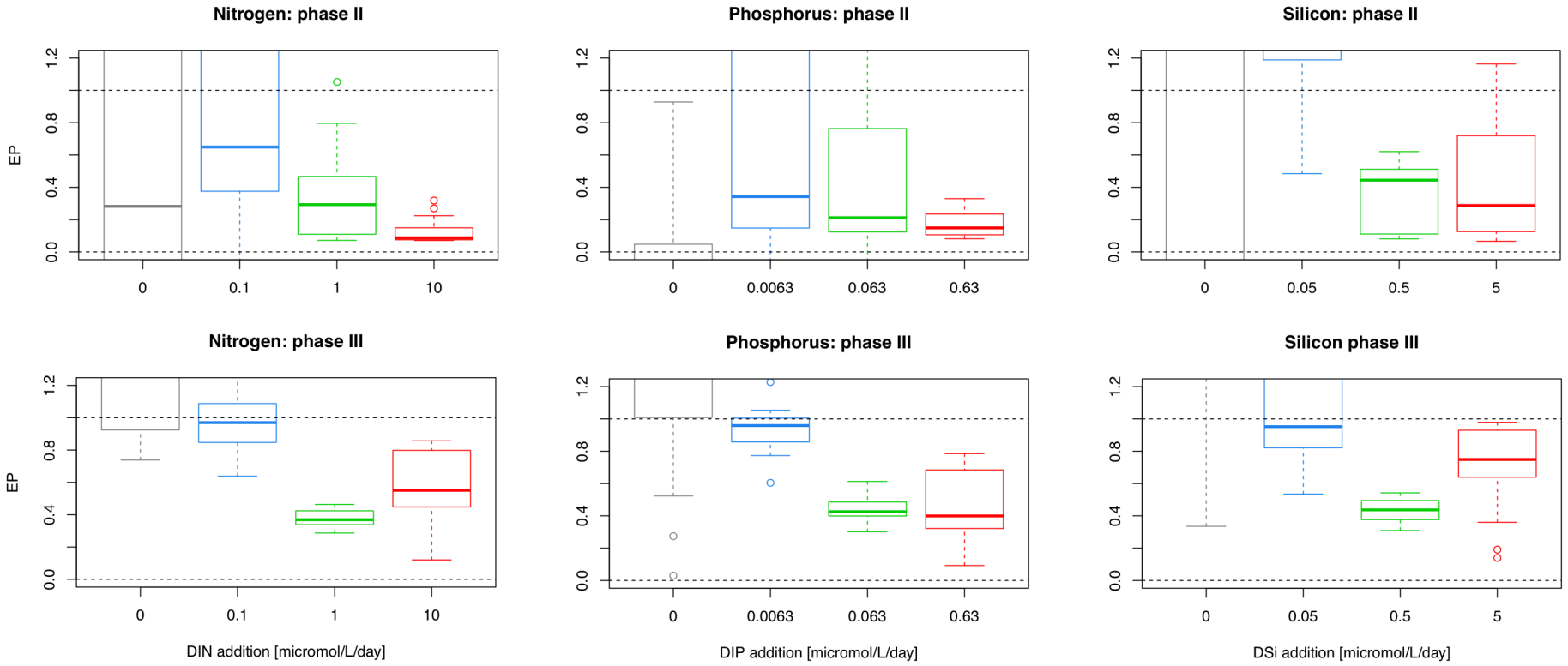


Figure 4.6b: **Export potential vs. nutrient addition**. Boxplots depict EP estimated via N (left plots), P (middle), and Si pools (right) for all treatments (control, low, medium, high). Data is integrated over phase II (upper plots), and phase III (lower plots) for each nutrient. Values of treatment mesocosms are pooled.

5 Discussion

5.1 Temporal development in N, P, Si elemental pools

5.1.1 Nutrient uptake

Our findings show distinct differences in the development of the three major elemental nutrient pools in our four treatment levels.

The high treatment, which experienced massive nutrient addition resulting in a rapid increase in Chl *a*, became carbon limited before any of the other nutrients could have become limiting. The increase of inorganic nutrient concentrations until t7 meant a higher input than uptake rate of DIN, DIP, and DSi (see Fig 4.1.1). Later, until t12, the uptake rate was higher than input rate. Phase II was a time of very high productivity with higher photosynthesis than respiration rates, and high nutrient uptake rates. When taking up charged nutrient species like nitrate, autotroph organisms also take up H^+-ions ('*nutrient-H^+-compensation-principle*', see Wolf-Gladrow et al., 2007) which causes an increase in total alkalinity and in pH. This increase was also seen in our high treatment mesocosms. The associated carbon uptake caused a decrease in pCO_2. Due to the strong C fixation by phytoplankton on the one hand, and the low resupply of CO_2 on the other hand, the high treatment mesocosms became carbon limited from ~t11 on, thus causing the end of the bloom phase. Fixed and exported C was taken out of the system (pumped out of the sediment trap), thus the only C source to the system was via air-sea gas exchange. However, the resupply by the atmosphere was slow, CO_2 being a gas with low water solubility. Additionally, the roofs of our mesocosms caused a decrease of wind speed at the air-sea interface, thus slowing down air-sea gas exchange even further (Wanninkhof, 1992). That the high treatment mesocosms were in fact C limited was proven by a side experiment. Two 20 L carboys were filled with mesocosm water from M2 and M5 on t23, enriched with CO_2, deployed in the respective mesocosm, and left there for about a week. Subsequently, inorganic nutrients were measured, and a few days after CO_2 addition, nitrate was taken up again in both of the carboys, yielding the proof for CO_2 limitation.

The medium treatment was limited by N and Si addition from the beginning of the bloom on, and probably experienced a shift to C limitation at the very end of the experiment. The initial nutrient peak occurred earlier than in the high treatment (from t5 to t7), and was followed by very low N, P, and Si concentrations. After t23, pCO_2 dropped to values <50 μatm in both mesocosms. Thus, we conclude that due to low pCO_2 growth conditions became less favourable in the medium treatment at the end of the experiment.

The low treatment which experienced the lowest NA, was mostly N limited throughout the experiment. Despite this limitation there was a decrease of DIP and DSi over time, with DIP decreasing from the beginning on while DSi decreased during the second half of the experiment. The phytoplankton community in M3 and M8 was mainly composed of the diatoms *Guinardia striata* and *Leptocylindrus df. minimus* (see Appendix, Fig 7.6). In the second half of the experiment, they formed a small diatom bloom which was not only mirrored in the phytoplankton data but also in the Si mass balance. Diatoms usually possess a lower N:P ratio compared to the canonical Redfield ratio of 16:1 (Geider and La Roche, 2002; Sarthou et al., 2005). A low N:P uptake ratio of these species could explain the decrease of phosphate over time. Another explanation could be nitrogen fixation as an additional N source to the system. In fact, a taxon known for N-fixation, *Trichodesmium*, was found in all mesocosms except for M8 on t1. However, *Trichodesmium* showed very low biomass, under 0.6 μg C/L. Additionally, *Trichodesmium* was only found in one of the low treatment mesocosms, and not in any of the mesocosms in samplings after t1. Thus, it could only have provided atmospheric N_2 as N source to the mesocosms at the very beginning. On top of that, typical daily N-fixation rates around Gran Canaria are in the nanomolar range (<5 nmol/L/day; Paul, personal communication). Therefore we argue that N-fixation did not play an important role in the experiment, and a low N:P uptake ratio was more likely the reason for the decrease of phosphate over time. The decrease of DSi can be explained by the low N:Si ratio of our nutrient addition of 2. Diatoms usually show higher N:Si ratios than that (Brzezinski, 1985). We assume this is why DSi decreased in the second half of the experiment.

The control treatment shared similar features with the low NA treatment: N limitation with a decrease of P and Si over time. Here, however, no nutrients were being added artificially. To incorporate the P and Si into biomass, nitrogen is needed though. To consume the starting concentration of ~0.08 μmol/L phosphate in the control mesocosms, ~1.28 μmol/L N were necessary, assuming a nutrient uptake ratio according to Redfield. The typical N-fixation rates for Gran Canaria of 5 nmol/L/day would not have been sufficient to provide the amount of nitrogen to the system necessary to fix the initially found phosphate and silicate in the given time. It is assumed there might have been initial concentrations of DON and DOP which were not detected by our measurements, and subsequently used for the build-up of PM. This will be discussed in detail in Sect. 5.2.2.

5.1.2 Development of chlorophyll a concentrations

The ~3 fold decrease of Chl *a* in all treatments after the filling of mesocosms could have been caused by e.g. mechanical stress when filling the mesocosms, or changes in turbulence or

in grazer control compared to the open water column. Another reason could have been a change in the light regime that the phytoplankton, which we caught in the mesocosms, experienced. Due to vertical mixing, the light regime in the open water column had probably been lower for the photoautotrophs. A downregulation of Chl *a* might have been their response to the higher light regime in mesocosms.

Increases in Chl *a* concentrations as response to nutrient enrichment has been reported by multiple studies (e.g. Gismervik et al., 2002; McAndrew et al., 2007; Meyer et al., 2016; Schlüter, 1998; Stibor et al., 2004). Schlüter (1998) constantly resupplied the inorganic nutrients NO_3^-, PO_4^{3-}, and SiO_4^- in their mesocosm approach, in a manner that nutrients were never completely taken up. This resulted in Chl *a* concentrations of up to 35 μg/L about a week after the first nutrient addition. This is in accordance with our high treatment level where maximum Chl *a* concentrations of ~40 μg/L were also reached about a week after the first NA. After the bloom peak, concentrations decreased in phase III due to C limitation. We argue that grazing control, which could have been another reason for the decline in Chl *a*, did only play a minor role here. This is because mesozooplankton abundances in the high NA mesocosms decreased to values lower than in all other mesocosms during phase III (see Appendix, Fig 7.4). Interestingly, a decrease in mesozooplankton biomass as a response to high amounts of nutrient addition has already been described by Gismervik et al. (2002). They assume that large and 'unhandy' diatoms in their two highest treatment mesocosms (1.27 and 2.16 μmol N addition/L/day) were responsible for the levelling off of mesozooplankton biomass. We rather assume that the carbon limitation and its implications on carbonate chemistry and food quality is responsible for the decline of mesozooplankton in our high treatment enclosures, though.

In the medium treatment mesocosms Chl *a* concentrations increased over time, peaked at t25, and decreased towards the end. The mesozooplankton, despite reaching very high biomass, was not able to catch up and graze down the phytoplankton community until the bloom had its peak. From then on, we suppose that low CO_2 availability paired with grazing of mesozooplankton was the cause for the decline of Chl *a*.

Compared to the medium and high NA treatments, the low treatment experienced no strong accumulation of Chl *a* (only slightly higher than in the control scenario). Despite the constant daily nutrient addition, Chl *a* concentrations stayed below 1 μg/L. We believe that high trophic transfer efficiency is the main reason for this. While microzooplankton biomass in the low treatment was low (mostly < 6 μg C/L; Stoltenberg, pers. comm.), overall mesozooplankton

biomass was at times comparable to that in the medium and high treatments (see Appendix, Fig 7.4).

5.2 Productivity and utilisation of nutrients

5.2.1 Net community production

Our data indicates that NCP did not increase linearly with nutrient addition. Due to the really low amount of added nutrients, NCP in the low treatment was not much higher than in the control treatment. Note that only 2.5 μmol/L NO_3^- were added to the low treatment in the course of 25 days. Another reason therefore could have been top-down control in the low treatment which inhibited high phytoplankton biomass build-up despite higher productivity than in the control scenario.

Medium and high treatments on the other hand showed a substantial increase in NCP compared to the lower treatments. However, despite the higher NA the high treatment did not show persistently higher NCP than the medium treatment. The reason for this is the carbon limitation in the high treatment mesocosms starting with phase III. We suppose that if the high treatment had not been C limited, its NCP would have been higher in phase III. However, we deem it unlikely that even without C limitation in the high treatment NCP would have increased linearly with NA. Some other variable would have become limiting, most likely light. A further increase in light absorption by increasing abundances of bloom forming primary producers, as well as the accompanying increase in chromophoric dissolved organic matter (CDOM) concentrations, would have likely caused the critical depth to become shallower, resulting in light limitation for phytoplankton.

5.2.2 Nutrient utilisation efficiency

According to our expectations, high nutrient addition resulted in low nutrient utilisation efficiency. In the high treatment, the added nutrients were used least efficiently during phase III due to the carbon limitation. During the time of C limitation, P was the nutrient that was taken up most efficiently in the high treatment. It is assumed that after the bloom had ceased, Si was not needed any longer by the C limited diatoms. Higher NUE_P (0.41 on t29) than NUE_N (0.48 on t29) indicates a lower than Redfield N:P uptake ratio.

Added nutrients were taken up most efficiently in the medium treatment. After around five days of nutrient addition, added nutrients were utilised faster than they were provided. This is comparable to the results from Taucher et al. (2017), who conducted a mesocosm experiment off the coast of Gran Canaria in 2014. Within five days following the addition of nutrient-

replete deep ocean water to an oligotrophic plankton community, ~3.15, 0.17, and 1.60 μmol/L nitrate, phosphate, and silicate were taken up by the community, respectively. In our intermediate treatment 5.0, 0.315, and 2.5 μmol/L nitrate, phosphate, and silicate, respectively, were taken up in the five days following the first NA. The efficient utilisation of nutrients lasted until the end of the experiment. However, we argue that if the experiment had continued for longer, the medium treatment mesocosms would probably have shared a similar fate as the high treatment mesocosms: they would have encountered carbon limitation, the primary producers being unable to utilise the added nutrients any longer. Additionally, the zooplankton probably would have caught up and grazed down the phytoplankton community.

During times of blooming events, the utilisation of added DSi in the medium and high treatment was more efficient than the utilisation of added DIN. The reason for this is probably the same one as for the DSi decrease over time in the low treatment (see Sect. 5.1.1). The N:Si ratio of nutrient addition was 2 while the stoichiometric ratio of the occurring bloomers was supposedly lower than that. This is supported by the results from Brzezinski (1985), according to whom the common diatom N:Si stoichiometric ratio is around 1. Thus, we assume that the bloom forming diatoms used up a higher proportion of the added silicic acid than of the added nitrate.

The low treatment started with a low NUE and became more efficient over time. A reason for this could be that there were initially not enough nutrients for bloomers to take off. Instead, small picophytoplankton was abundant during phase II (see Appendix, Fig 7.5) while larger diatom species followed in succession. A similar succession was reported by McAndrew et al. (2007) who found a shift from small picophytoplankton (<2 μm) to larger (>10 μm), Si-utilising photoautotrophs in their deep water nutrient enrichment experiments. In phase III the already mentioned small diatom bloom occurred (see Sect. 5.1.1). We assume the diatoms used the available nutrients more efficiently than the smaller picophytoplankton, and thus caused an increase in NUE. This blooming event was also the reason for the delayed increase of NUE_{Si} compared to NUE_N and NUE_P. NUE_N, did not reach very high efficiencies in the low treatment throughout the experiment. The main reason for this is the problematic NH_4^+ data (NH_4^+ measurements will be discussed in Sect. 5.4.1). Ammonium almost entirely made up the DIN starting conditions in M3 and M8 (starting condition: 0.73 μmol/L DIN, of which 0.57 μmol/L were NH_4^+, averaged for M3 and M8 and from t1 to t4). The ammonium data is considered to be overestimated in this case, though, since ammonium is usually taken up and cycled rather quickly and since it usually is the preferred N source for primary producers, especially when nitrate concentrations are low. Because of the overestimated NH_4^+ starting conditions, NUE_N

was thus not able to reach very high efficiencies. The strong impact of ammonium on NUE_N becomes evident when noticing that every decrease in NUE_N correlates with an increase in NH_4^+ concentrations.

5.3 Effects of nutrient addition on export potential

5.3.1 Export fluxes

Our experiment showed that the higher the nutrient addition, the higher the export flux. This increase was not a linear one though. The 10 fold increase of NA from the low to the medium treatment resulted in a ~2 fold increase in total PM_{sed} flux (factors for the different nutrients: PON_{sed}: 2.4; POP_{sed}: 1.5; BSi_{sed}: 2.8), and the 100 fold increase of NA from the low to the high treatment resulted in a ~10 fold increase in PM_{sed} flux (PON_{sed}: 9.7; POP_{sed}: 5.5; BSi_{sed}: 13.4). We believe that this non-linear increase in export flux is due to carbon limitation in the high treatment in phase III, and the low proportion of PM_{sed} to suspended matter in the medium treatment. A longer experimental duration would have probably caused a much higher total export flux in the medium treatment due to the termination of the phytoplankton bloom and its following export event.

When comparing the export at the approximate bloom peaks of the medium treatment (t25) with the high treatment (t12), the data suggests that the export of the two treatments at the same developmental stage is not very different (Table 2). However, at the point of the bloom peak, about four times less nutrients had been added in total to the medium treatment (21 μmol/L NO_3^- in total) than at the respective point in time to the high treatment (80 μmol/L NO_3^-). This indicates that the export of added nutrients to the sediment trap was more efficient during the bloom development in the medium compared to the high treatment. Due to the high variability within the high treatment level though, this remains only a suggestion.

		ΣPON(sed)	ΣPOP(sed)	ΣBSi(sed)
		µmol/L		
T12	M2	3.73	0.19	3.42
	M5	8.05	0.32	8.10
T25	M4	5.68	0.31	4.09
	M7	4.35	0.33	3.56

Table 2: **Comparison of the accumulated sedimented PON, POP, and BSi** concentrations in the high treatment mesocosms (M2 & M5) of t12 and the medium treatment mesocosms (M4 & M7) of t25.

5.3.2 Export potential

The export potential was highest in the control, low and high treatments, and lowest in the medium treatment. Our expectations were though, that EP would increase with increasing nutrient addition owing to increased marine snow formation, phytodetritus aggregation, and fecal pellet production. One reason for the low EP in the medium treatment, despite its high utilisation of nutrients, is that a lot of the added nutrients were transferred to higher trophic levels and thus could not sink out of the mesocosms (see Appendix, Fig 7.4). Another reason is that the phytoplankton bloom which consisted mainly of the diatom *Leptocylindrus*, had only just reached its peak at the end of the experiment. Diatom blooms are usually followed by export events. Thus, it is very likely that EP would have increased after the termination of the bloom. The increase of EP in M4 from t27 to t29 which is also reflected in the $PM_{susp/sed}$ data, hints at that.

EP in the high treatment was persistently higher than in the medium treatment. Due to the rapid phytoplankton growth during phase II, mesozooplankton was probably not able to catch up and graze down the phytoplankton community. Since mesozooplankton abundances declined drastically during phase III (see Appendix, Fig 7.4), we assume that trophic transfer efficiency was less efficient than in the medium treatment (Spisla, pers. comm.). Consequently, we assume that a substantial proportion of the carbon limited phytoplankton community was exported to the sediment trap via aggregate export following the bloom phase. Interestingly, the export behaviour of our high treatment is similar to that of communities in the mesocosm experiment carried out by Svensen et al. (2002), which received only one or two pulses of nutrient addition. When investigating the effect of the mode of nutrient supply on the vertical flux of biogenic matter, they found that these mesocosms rather resembled spring bloom-like systems with high Chl *a* concentrations and high sedimentation rates. Continuous nutrient addition on the other hand resulted in more regenerative systems with low and stable export fluxes. This rather applied to our medium treatment level. However, the rate of NA was a lot higher in our high treatment mesocosms than the overall addition carried out by Svensen et al. (15 μmol/L NO_3^- added over 19 days). To this rate of NA, only our medium treatment level is comparable (25 μmol/L NO_3^- added over 25 days).

The EP minimum during phase II followed by a subsequent increase of EP in the two highest treatments was caused by an increase of PM_{susp} after the first nutrient addition, followed by a delayed increase of PM_{sed}. At the beginning of the nutrient addition, DIM accumulated in the medium and high treatments and primary producers were able to potentially grow exponentially. They grew until their biomass could utilise more than the amount of added

nutrients per day. Consequently, the accumulated DIM was used up, and phytoplankton growth became limited by the rate of NA. The leftover biomass died off and sank, which is reflected by the small PM_{susp} peak on t9 in the medium treatment. Because of the higher rate of NA this happened at a later stage in the high treatment.

Our results suggest that in the low treatment almost all produced biogenic matter was exported. However, the low treatment was also characterised by the highest trophic transfer efficiency (Spisla, pers. comm.). This is a contradiction since nutrients can either be transferred very efficiently to higher trophic levels or exported very efficiently but not both. It is assumed that NCP in the low treatment was underestimated and EP thus overestimated. One cause for this is that mesozooplankton was not accounted for in the PM_{susp} pool. Boxhammer et al. (2018) showed in their mass balance approach that mesozooplankton temporarily contributed to up to 20% of particulate phosphorus, and thus should not be neglected in the suspended PM pool. Especially in the low treatment, with comparatively high mesozooplankton abundances (see Appendix, Fig 7.4) and low NCP, the overestimation of NCP would lead to a high distortion of the EP parameter.

There were 'impossible' values in both the control and the low treatment levels ($EP > 1$ and $EP < 0$). These occurred when PM_{susp} starting conditions were higher than PM_{susp} concentrations throughout phases II and III. Then, either NCP became smaller than PM_{sed}, resulting in EP values > 1, or NCP was smaller than 0, resulting in EP values < 0.

5.4 Mass balance approach

The investigated mass balances of the three major nutrient pools N, P, and Si often did not close in our mesocosms. In the high and medium treatments NCP was lower than the sum of utilised nutrients (ΔDIM). While in the low and control treatments NCP was higher than ΔDIM (with the exception of the Si mass balance in the control scenario). That mass balance calculations are challenging even in enclosed mesocosm systems has recently been reported by Boxhammer et al. (2018). The discrepancies in our mass balance approach were most likely caused by methodological errors. Hereafter, the possible methodological errors that have occurred on either the NCP side of the mass balance or the ΔDIM side or both will be discussed.

5.4.1 Methodological discussion

Possible systematic errors occurring on both sides of the mass balance:

A critical step for data acquisition is the sampling step which often involves unnoticed systematic errors. Since we took integrated water samples of the water column with 2 m

sampling tubes, it was necessary to mix the tubes before filling our bottles. One possible error source occurring on both sides of the mass balance is improper mixing of the sampling tube. Though a mixing test for our sampling tubes was carried out in the middle of the experiment, we neglected to conduct one before the beginning of the experiment. The test revealed that the mixing of water inside the tubes was probably insufficient (Spisla, pers. comm.). Subsequently, greater attention was paid when mixing the samples. However, our CTD data suggests that the water column was vertically homogeneously mixed throughout the experiment which suggests that the mixing error was probably minor.

A carry-over effect by the sampling tube, and thus an overestimation of DIM in the lower treatments, is unlikely because we adhered to a sampling order from low to high NA mesocosms throughout the experiment. Additionally, sampling tubes were cleaned regularly.

Possible errors occurring on the ΔDIM side:

Since a known amount of nutrients was added to three of our treatments, we can more or less estimate whether or not our inorganic nutrient measurements were accurate. The overall consumed DIM in the low and medium treatments mirrored their nutrient additions quite well. For instance, we added a total of 25 μmol/L nitrate to the medium treatment and around 25 μmol/L N had been taken up on t30 in the medium treatment mesocosms according to our DIN measurements (see Fig 4.3.1). Additionally, the DIN increase in phase III in the C limited high treatment oftentimes mirrored the daily NA of 10 μmol/L nitrate. Therefore, the potential error on the ΔDIM side is believed to be lower than the one on the NCP side.

Nevertheless, measuring dissolved inorganic nutrients can involve several pitfalls. For instance, applying too much pressure when filtering DIM samples can lead to breaking up cells, which in turn can lead to an overestimation of DIM concentrations. Contamination is another error source that can arise from wrong sample handling and has the highest impact on samples with low inorganic nutrient concentrations. We assume that contamination is the reason for the homogeneity between treatments in the NH_4^+ data. It is assumed that a systematic error occurred throughout the experiment during sample handling and/or measurements of NH_4^+ samples. Due to the compound's high water solubility, contamination is a common problem for ammonium samples. The longer ammonium samples are exposed to air and the lower the sample volume and its concentration in the sample, the higher the influx of ammonia into the vials. Our filtrated inorganic nutrient samples were exposed to the atmosphere in small 10 mL vials before measurements. We assume that during this time the samples were contaminated by equilibration with the atmosphere, which masked our NH_4^+ signals.

Apart from the possible contamination of ammonium data, we assume our inorganic nutrient measurements are reliable. This is because we took great care during sample analysis, and followed the procedures by Grasshoff et al. (2009) and the GO-SHIP Repeat Hydrographic Manual (Hydes et al., 2010) when measuring nutrient samples. We diluted samples with concentrations exceeding standard concentrations, thus we did not measure outside standard calibration ranges. We also measured CRMs (certified reference materials) to test for accuracy, and triplicates to calculate standard deviations and check for precision of our measurements.

However, the LODs for our inorganic nutrient measurements are quite high (see Table 5.4.1). This is really only a problem for the control, and, to a lower extent, for the low treatment. In the higher treatments, the NA of one day already provides enough nutrients to overcome the detection limits. In the low treatment level however, the overall Si addition was 1.25 μmol/L and thus not much higher than the mean silicic acid detection limit. Therefore, we can make statements as to whether or not the added nutrients were taken up but we cannot safely say whether they were fully taken up or not. This is more problematic in the control mesocosms, where no nutrients were being added and, except for phosphate, nutrient concentrations were almost entirely under the LOD. The consequence is that we were oftentimes merely able to state that DIM concentrations were very low but were unable to describe precise temporal developments. This might have caused an underestimation of ΔDIM in the control and low treatments, and might thus help to explain that NCP > ΔDIM in most of their mass balances. The only mass balance in which NCP < ΔDIM is the Si mass balance in the control treatment. We believe this discrepancy was overestimated due to the high temporal variation in the data (see Fig 4.3.3). This variation was caused by measuring low DSi concentrations in proximity to the LOD. In fact, the estimated initial DSi concentrations (0.84 μmol/L and 0.83 μmol/L for M1 and M6, respectively (averaged between t1 - t4)) were about as high as the accumulated sedimented BSi concentrations at the end of the experiment (0.80 and 0.93 μmol/L Bsi_{sed} in M1 and M6, respectively). This indicates a good match between taken up inorganic nutrients and built-up biomass.

	nitrate + nitrite	silicic acid	nitrite	phosphate	ammonium	TDN	TDP
LOD	0.444	0.971	0.033	0.034	0.055	0.888	0.706

Table 5.4.1: **LODs for the measured total dissolved, and dissolved inorganic nutrients** in μmol/L. Displayed are mean values calculated from the LODs of each measurement day.

Finally, we argue that due to our quality control the dissolved inorganic nutrient data can be considered accurate for the medium and high treatment. In the control treatment however,

our measurement range does not enable us to make precise statements on temporal DIM developments. Whilst this is also a problem in the low treatment it is not as severe due to the nutrient addition resulting in higher DIM concentrations.

Possible errors occurring on the NCP side:

Since we believe our DIM measurements to be accurate for the two higher treatments, NCP is believed to be the parameter containing the most severe sources of error. These are manifold, since many different methods were used to assess this parameter. First of all, CRMs neither exist for our DOM nor for our PM measurements. Therefore, we cannot be sure our samples were measured accurately. Additionally, we did not perform replicate measurements for suspended BSi at all and only on a couple of days for suspended POP. Thus we cannot assess the precision of the measurements of these parameters either.

Dissolved organic matter:

Our DOM data turned out to be highly problematic. This is due to several difficulties we encountered when measuring DOM on Gran Canaria. First of all, filters with different pore sizes were used for DOM (0.75 μm) and DIM (0.45 μm) measurements. This results in an overestimation of DOM compared to DIM. Secondly, DOM and DIM samples were not measured on the same day. DOM samples were instead frozen after filtration and measured after the experiment. Thirdly, DOM samples of the high treatment were not measured diluted because of a mistake during the dilution process. Therefore, the concentrations were often higher than the highest standard (50 μmol/L NO_3^-) and thus measured out of calibration range. Lastly, the proper Molybdat solution for DOP measurements was not readily available. The needed solution was prepared by hand. Having finally measured the samples and processed the data, we noticed that there are many negative DOP values which occurred in all treatments as well as one negative DON value in the high treatment (see Appendix, Fig 7.1 & Fig 7.2). When analysing DOM, one measures TDM and subtracts DIM from it. The outcome can be negative when you either overestimate DIM or underestimate TDM concentrations. The same problem occurred with the DON/DOP data in the 2017 KOSMOS experiment in Peru (Meyer, pers. comm.). Just like in our study, the DOM samples were frozen and measured independently of the DIM samples. It turned out that, when measuring DIM in DOM samples from a specific sampling day, concentrations at times varied strongly from DIM measurements from that day. The driving factors for this were identified as the different sample treatments of DIM and DOM samples (filtration, freezing, Quaatro adjustment). We suppose that these are also the reasons

for the negative values in our DOM data. Consequently we suggest in order to obtain accurate DON/DOP data that DOM and DIM samples are treated equally and are measured on the same day.

Another problem, especially for the DOP data, is the high LOD. Most of the DOP values were below the detection limit (see Appendix, Fig 7.2). Furthermore, the DON/DOP variability within treatments was very high, as well as the variability over time in the control and low treatments. These fluctuations were not reflected in any of the other nutrient pools, and at times they distorted the mass balances heavily which is why we decided not to account for DOM in the N and P mass balances. The precise determination of the DOM pools turned out to be one of the major challenges for the mass balance calculations of Boxhammer et al. (2018) as well.

Fortunately, there is less problematic data on dissolved organic carbon (DOC) from the experiment (see Appendix, Fig 7.3). DOC concentrations rose to very high values in the medium and high treatment levels (up to >500 μmol/L) and showed a slight increase over time in the control and low treatment (100 - 200 μmol/L). However, simply extrapolating DOC concentrations according to the Redfield ratio to obtain DON and DOP concentrations is impracticable. Studies suggest that DOM stoichiometry is highly variable and oftentimes strongly uncoupled from the canonical Redfield ratio (Deutsch and Weber, 2012; Hopkinson and Vallino, 2005). Although not being able to calculate elemental DOM partitioning, it is still likely that an increase in DOC is accompanied by an increase in DON and DOP. Therefore, we assume that the DON/DOP concentrations increased with rate of nutrient addition as well, with low concentrations in the control and low treatment, and high concentrations in the medium and high treatment levels. Our analysed DON data also shows this trend.

Furthermore, missing DON and DOP could be a reason for the discrepancies in the low and control treatments. Dissolved organic matter is typically found in higher concentrations than DIM in oligotrophic regions (Church et al., 2002). DON and DOP could initially have been abundant in the mesocosms which we did not notice due to our measurement issues. This was then utilised and converted to POM and subsequently showed up in our mass balances. About 1 - 2 μmol/L DON and 0.1 - 0.2 μmol/L DOP would have been necessary to account for the missing N and P in the mass balances of the control and low treatments. These are realistic DON and DOP concentrations for an oligotrophic region.

To sum up, the missing DON and DOP data likely caused an underestimation of $NCP_{N/P}$ in the medium and, probably more severe, in the high treatment level. As an unaccounted for nutrient pool it might also be an explanation for the missing nutrients in the control and low treatment levels.

Suspended/sedimented particulate matter:

Not only the dissolved organic pool was problematic, also the particulate matter had its difficulties.

The most critical thing was probably the subsampling and processing of sedimented PM. Reasons for this are that we filtered a very small subsample (1 - 30 mL) from oftentimes huge sediment sample volumes (up to >10 L) to analyse PON, POP, and BSi. Since the samples were not always homogeneous, the corresponding subsamples were not always representative of the whole sediment sample. The accuracy of measuring such minute fractions of our sediment samples is disputable, at best. Additionally, the conversion from sediment volume to sediment dry weight was not done accurately. The density used for the calculation was the density of seawater (1.023 kg/L). However, sedimented material obviously has a higher density than seawater. This resulted in an underestimation of PM_{sed} dry weight, with the error increasing, the denser the sediment trap sample and the larger its volume. The higher this underestimation of PM_{sed}, the higher the underestimation of NCP in the mass balance. Hence, this systematic error probably had the highest impact on the NCP in the high treatment mesocosms. Apart from that, on some days we were not able to capture the entire sediment sample. On these occasions we sampled the leftovers on the next day, which enabled organisms to degrade material in the sediment trap over a longer period of time. We furthermore propose that in future studies the processing of sediment trap samples should be a different one. Instead of using a wet splitting technique resulting in a heterogeneous subsample, sedimented material should be processed by particle concentration, freeze-drying, and grinding to get a homogeneous sediment powder for further biogeochemical analysis. A detailed protocol for this was written by Boxhammer et al. (2016).

Inaccuracies can also be caused by the patchiness of suspended PM under strong marine snow formation. Since our sampling tube had an opening with a small diameter, this might have caused measuring inaccuracies in our high NA mesocosms. However, apart from the rare occasions of extremely high marine snow formation, we assume that the water column was homogeneously mixed and our PM_{susp} sampling was hence reliable. Other possible errors concerning PM processing include that OM < 0.75 μm was not accounted for, since we did not account for OM with our dissolved nutrient measurements and PON and POP were captured on filters with 0.75 μm pore size. In the high treatment mesocosms there were also some values of suspended PM higher than the highest measured standards. PON_{susp} values of M2 and M5 were above the highest standard on t15 but still far within the measurement range of the

elemental analyser. M2 was above the highest POP_{susp} standard on t13 and above the highest BSi_{susp} standard on t10, t12, and t13. This might have led to an underestimation of PM_{susp} in the high treatment and is thus another possible reason for the non-closing budget.

Concluding, we assume that the uncertainties concerning the assessment of sedimented PM are as substantial, if not more severe than the missing DON/DOP data. The accumulated PM_{sed} was oftentimes the biggest pool in our nutrient budgets, certainly involving at least two systematic errors (sediment subsampling and conversion of volume to dry weight). We assume that the missing DOM, together with the underestimated PM_{sed} data is the main reason for the discrepancies in the high and intermediate treatment mass balances.

5.4.2 Best fit

The mass balances with the lowest discrepancies were found in the low and in the medium treatment level. First of all, we assume that the DON/DOP concentrations in the high treatment were higher than in the medium treatment, causing a higher underestimation of NCP in the high treatment. Secondly, the lower discrepancy in the medium treatment speaks for the underestimation of the export flux (PM_{sed}) to be the main reason for the discrepancies in the high and medium treatments because the export in the medium treatment was low compared to the export in the high treatment. The low treatment, characterised by an even lower export flux, did not suffer from the PM_{sed} underestimation as much as the higher treatments. Also, the error caused by the proximity of nutrient concentrations to their LOD was less severe in the low than in the control treatment. Possible unaccounted for initial DON and DOP concentrations would have made a higher impact in the control treatment as well, since the low treatment received daily nutrient additions, which would have buffered such an error.

Besides the low and medium treatment levels, the silicon elemental pool turned out to have the lowest discrepancies of all three examined elemental mass balances. Note that the Si mass balance in the low treatment, despite being higher than the N and P mass balances in total in phase III, was lower than the N and P mass balances at the end of the experiment. The most obvious reason for the good fit in the Si budgets is that there was one nutrient pool less to assess when dealing with Si: dissolved organic matter. Since the DOM pool was one of the most problematic ones in this study, the Si mass balance did not suffer nearly as much under the methodological errors as the N and P budgets. The relatively lower discrepancies in the Si mass balances, especially in the medium and high treatments, point out the significance of the error caused by the missing DOM pool.

6 Conclusions and outlook

The objective of this study was to examine the effects of different rates of nutrient supply on nutrient export and nutrient utilisation efficiencies in the N, P, and Si elemental pools. What follows is an overview of the most important findings.

- *High treatment (10 / 5 / 0.63 µmol N, P, Si / L / day):*
  The high treatment was characterised by immense phytoplankton growth, which came to a stop due to CO_2 limitation. Although this caused a low overall nutrient utilisation efficiency, the treatment exported organic matter very efficiently. However, serious underestimations on the NCP side prevent us from making reliable quantitative statements on this.
- *Medium treatment (1 / 0.5 / 0.063 µmol N, P, Si / L / day):*
  The medium treatment showed favourable growth conditions for primary producers with very efficient utilisation of all three provided nutrients. The export potential, however, was relatively low. Instead of being efficiently exported to the sediment trap, biogenic matter rather remained in the water column. We suppose that if we had applied this rate of nutrient addition for a longer time period, the system would have developed higher export potential and a balance between phytoplankton growth and grazing control.
- *Low treatment (0.1 / 0.05 / 0.0063 µmol N, P, Si / L / day):*
  The low treatment was very efficient in utilisation of nutrients, and in transferring them to higher trophic levels. However, not enough nutrients were provided to fuel a proper phytoplankton bloom. Instead, high grazing control kept primary producers (and thus NCP) at bay. Besides trophic transfer efficiency, the estimated export potential was also very high, which is contradictory. We assume the real export potential was lower than our estimates.

What we encountered in the high treatment in terms of nutrient addition was an overkill for a small scale mesocosm experiment. However, if conducting artificial upwelling in the surface waters of the open ocean, there would be a resupply of CO_2 by upwelled water, as well as a strong dilution of surface water. Thus, it remains unknown whether or not such huge amounts of provided nutrients could be efficiently utilised in open waters. The medium level of nutrient addition resulted in favourable growth conditions and a low export potential.

Another study with the same approach and a longer experimental duration is needed to confirm our assumption that the system would have become more effective in exporting biogenic matter with time. When the goal is to efficiently export large amounts of carbon, we suppose the rate of nutrient addition of the high treatment level is sufficient. When the goal is pelagic fish production however, a rate of nutrient addition near the medium treatment level is more advisable. The low treatment on the other hand does not fulfil the requirements for either of the applications. Its overall production is simply too low. However, this treatment is interesting in ecological terms because of its high trophic transfer efficiency and the minor diatom bloom in the post-bloom phase, which was fuelled by very low nutrient conditions.

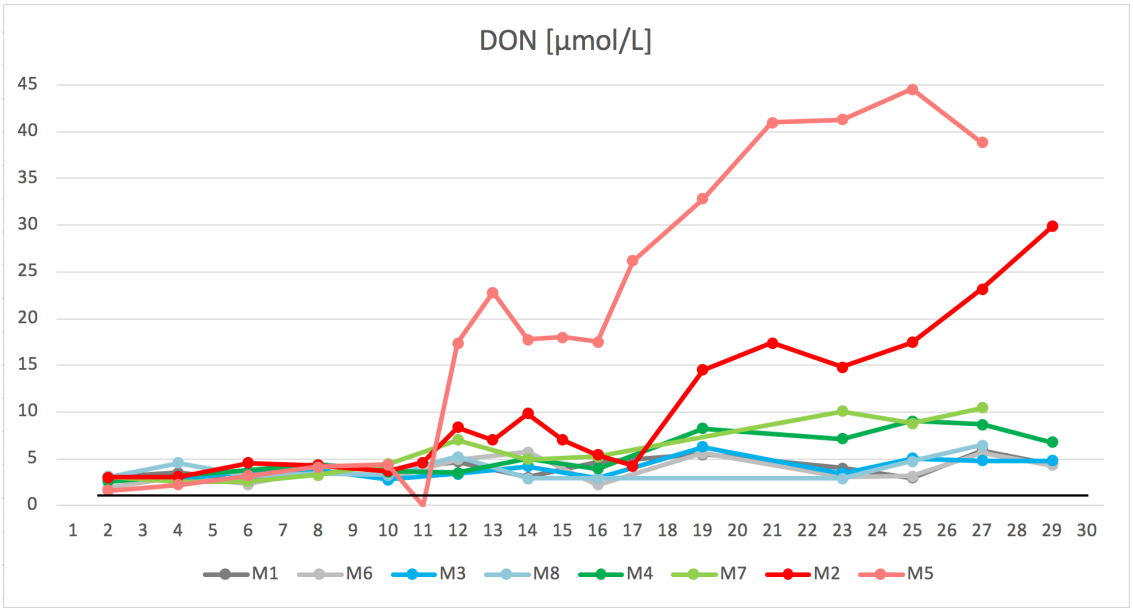
There are some methodological issues in this study which can be used to improve future experiments. The samples for dissolved organic nitrogen and phosphorus should be treated the same way as the samples for dissolved inorganic nutrients, and all dissolved nutrient measurements should be carried out on the same day. Instead of using a wet splitting technique, the subsampling and processing of sedimented matter should be performed as suggested by Boxhammer et al. (2016). Furthermore, mesozooplankton abundances should be accounted for in the PM pools, since they can make a significant contribution to the net community production. Lastly, ammonium samples should be exposed to the atmosphere as shortly as possible, especially at low sample volumes, and be processed quickly. These measures should ensure a more precise assessing of ΔDIM and NCP, and thus lead to smaller discrepancies in the N, P, and Si mass balances if performed correctly.

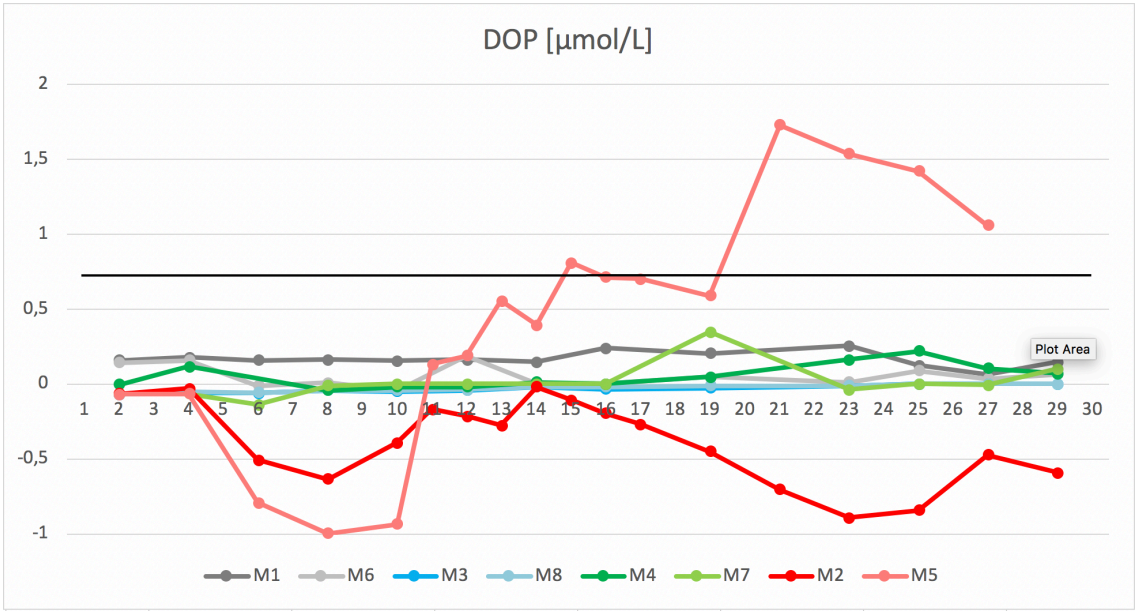
This study provides novel and valuable information in a at present largely unexplored research field of examining biological responses of whole pelagic communities to artificial upwelling. It has not only answered a lot of questions, but also brought up new ones. What would have happened if there had been no CO_2 limitation? What if the experiment had lasted longer? What is needed to answer these questions are follow-up studies with a similar experimental approach, but with larger water bodies to act against CO_2 limitation and a longer experimental duration to achieve stable conditions in all treatments. Furthermore, the export efficiency of particulate matter is controlled by the sinking velocity of particles and the particle remineralization rate. Thus, respiration and sinking velocity should be estimated to provide data on export efficiency that can be extrapolated to depths below the euphotic zone. Finally, a higher resolution of NA modes is required to detect the best mode for achieving high export potential.

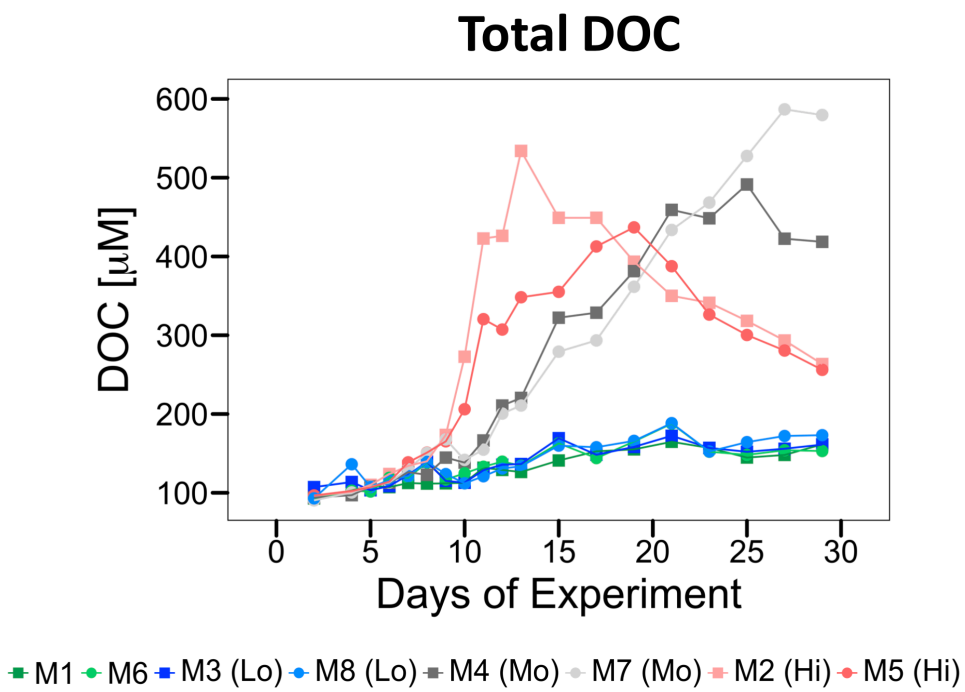
The processes controlling export efficiency in pelagic systems are complex, and the effect that intentional eutrophication has on them, are still a wide field for investigation. As the first step of the Ocean artUp project, which examines the possibility, feasibility, and potential side effects of artificially creating ecosystems as productive as upwelling systems, this study helped to understand if and how artificial upwelling can help to contribute to negative CO_2 emissions, while also assessing the possible risks and side effects of this promising approach.

7 Appendix

Dissolved organic matter:







Figures 7.1 – 7.3: **Dissolved organic nutrient concentrations** during the course of the study. Shown are total DON (top), DOP (middle), and DOC (bottom) concentrations in each mesocosm. Black horizontal bars in the DON/DOP graphs depict the LOD. Note the different colour code for DOC (red for high, grey for medium, blue for low, and green for control treatment mesocosms).
Data for DOC was provided by Nauzet Hernández, Isabel Baños, Márkel Gómez-Letona, and Javier Arístegui (Instituto de Oceanografía y Cambio Global, Universidad de Las Palmas de Gran Canaria).

Mesozooplankton:

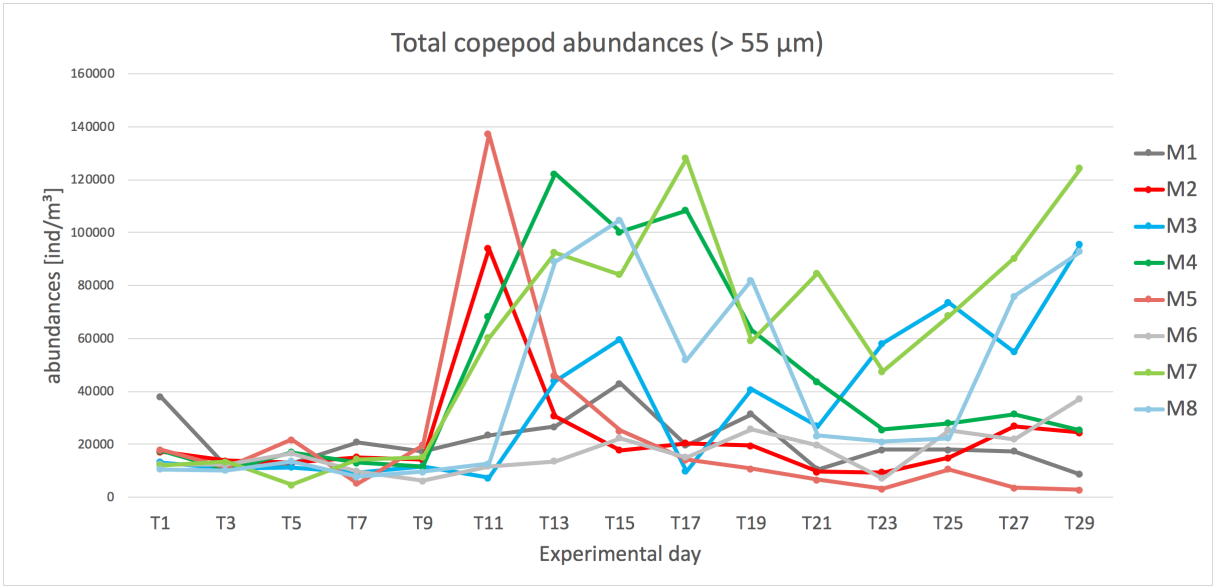


Figure 7.4: **Total copepod abundances** during the course of the study in each mesocosm. Includes the size classes 55-200, 200-500, 500-780, and >780 μm.
Unpublished data which is not quality controlled. Data was provided by Carsten Spisla (GEOMAR – Helmholtz Centre for Ocean Research Kiel).

Picoplankton:

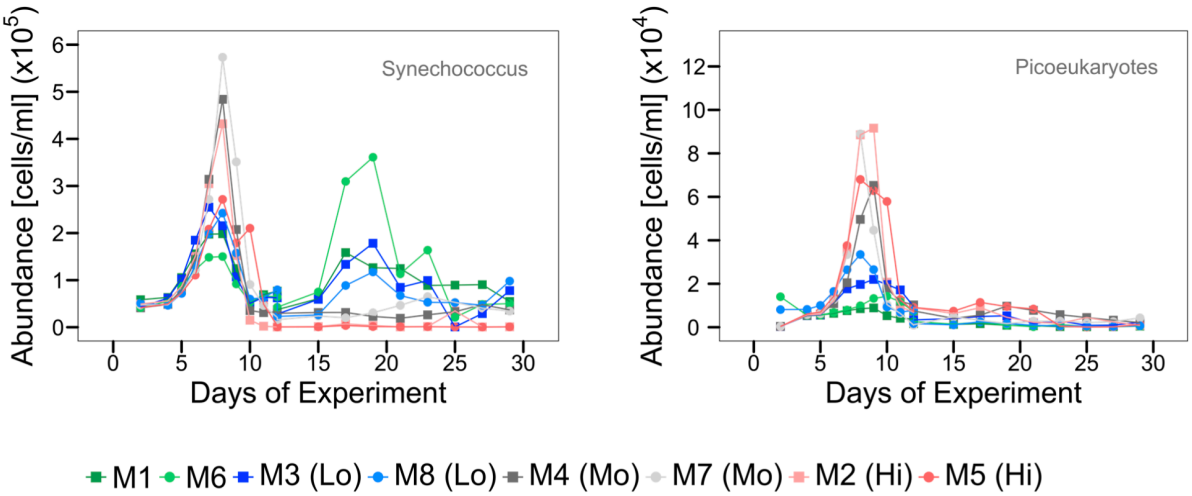


Figure 7.5: Synechococcus and picoeukaryote abundances during the course of the study in each mesocosm. Note the different colour code (red for high, grey for medium, blue for low, and green for control treatment mesocosms).
Data for picoplankton abundances was provided by Nauzet Hernández, Isabel Baños, Márkel Gómez-Letona, and Javier Arístegui (Instituto de Oceanografía y Cambio Global, Universidad de Las Palmas de Gran Canaria).

Phytoplankton:

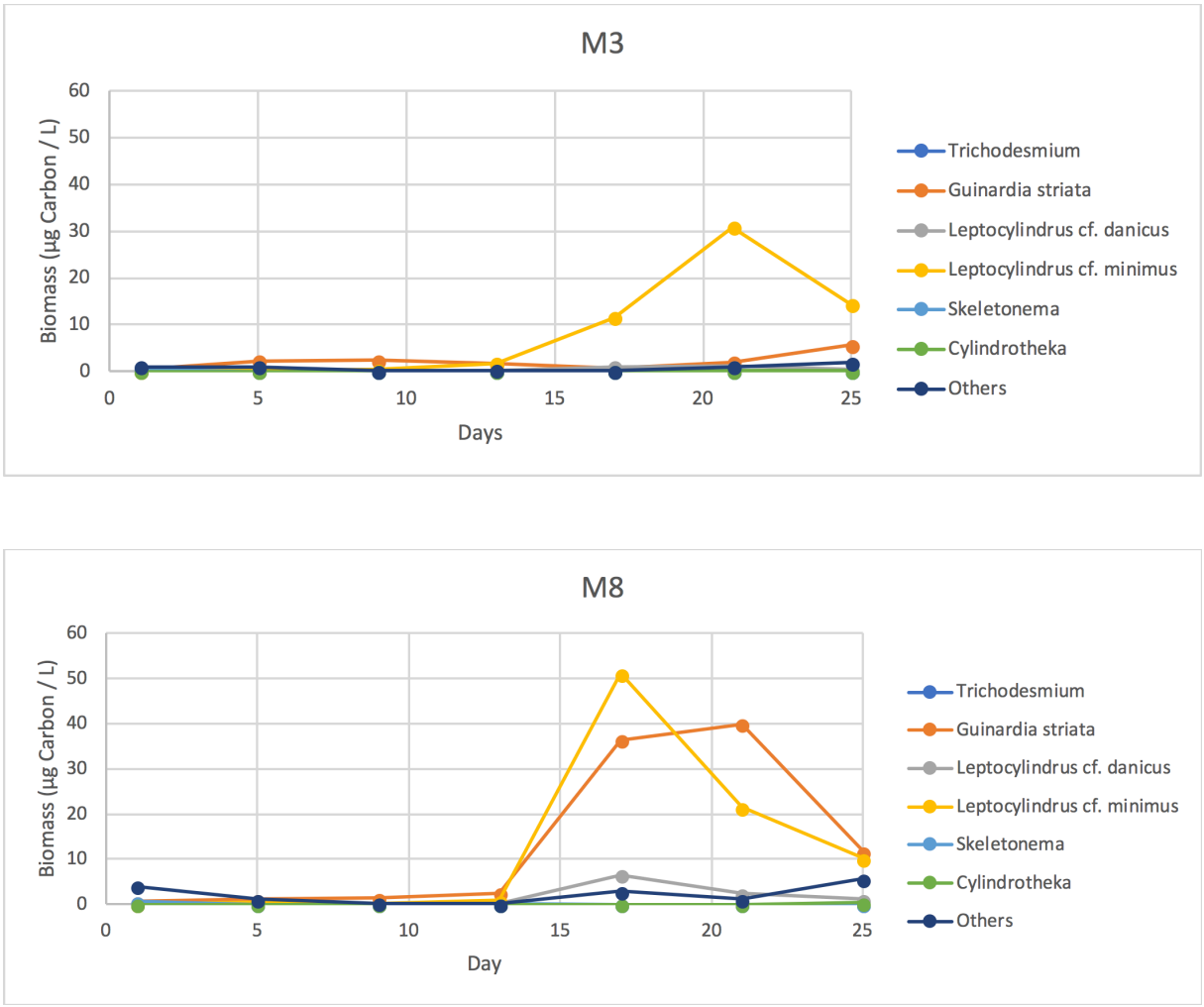


Figure 7.6: **Phytoplankton biomass per species in the low treatment** from the beginning of the experiment until t25. Data for the mesocosms M3 and M8 are displayed.
Unpublished data which is not quality controlled. Data was provided by Julia Raab (GEOMAR – Helmholtz Centre for Ocean Research Kiel).

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Acknowledgements

First of all, I would like to thank Dr. Jan Taucher for his continuous support and guidance throughout the making of this thesis. I consider myself lucky that I had you as supervisor.

I also want to thank Professor Ulf Riebesell for giving me the opportunity to work in his research group. Our conversations did not only help me understand my data better, they were also a constant source of motivation.

Thank you Dr. Mark Lenz for enduring my endless questions concerning statistics.

Thank you Andrea Ludwig and Jana Meyer for enduring my endless questions concerning pretty much everything.

I also want to thank Dr. Allanah Paul and Dr. Michael Sswat for their helpful and honest feedback.

Furthermore, the input and the suggestions I received from Dr. Judith Meyer, Carsten Spisla, and Dr. Lennart Bach enabled me do understand and interpret the more complex results of data.

I also want to thank the whole Gran Canaria 2017 team for an amazing experience. See you next time!

Last but not least, I want to sincerely thank my mom and sister, who encouraged me in times of need. It would not have been possible without you.