PROPAGATION OF EXTREME EVENTS:

The effect of nutrients on the bloom dynamics and spatial propagation of harmful dinoflagellates

Dissertation

zur Erlangung des Grades und Titels eines
DOCTOR RERUM NATURALIUM, Dr. Rer. Nat.

Angenommen durch
die Fakultät Mathematik und Naturwissenschaftlichen
der Carl von Ossietzky Universität, Oldenburg

Von
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Geboren am 23.08.1988 in Göttingen

Oldenburg, 30 April 2019

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Tag der Disputation: Oldenburg, 30 April 2019

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General Introduction

Harmful algal blooms (HABs)

Marine phytoplankton contributes less than 1% to the global photosynthetic biomass, but it is responsible for approximately 50% of the world's net primary production (Bar-on et al., 2018; Falkowski et al., 2004; Field et al., 1998). As a part of the biological pump, it plays an important role in the global carbon pool as well as the global climate (Basu and Mackey, 2018; Falkowski et al., 2000). Marine phytoplankton constantly takes up large amounts of atmospheric CO_2, and the current CO_2 concentration of around 400ppm would have been much higher without the biological pump (Falkowski et al., 2000; IPCC, 2013). About 25% of the carbon, which is fixed by phytoplankton in the upper water column, sinks to the bottom of the ocean as non-degraded organic matter or as zooplankton faecal pellets, where it can withstand bacterial degradation (Falkowski et al., 2000; Turner, 2015). The marine ecosystem is thus a major sink for atmospheric CO_2, removing approximately one-third of anthropogenic CO_2 emissions from the atmosphere (Basu and Mackey, 2018; Sabine et al., 2004; Turner, 2006).

Some phytoplankton species can have larger influences on food web dynamics than other species (Fig. 1). The production of toxins, for instance, can cause severe damage or kill higher trophic organisms, such as fish, mammals, birds and humans (e.g. Granéli and Turner, 2006). In fact, also nontoxic algae can have harmful effects, as they can clog or injure fish gills or lead to oxygen depletion through microbial decomposition after massive blooms (Granéli and Turner, 2006). These Harmful Algae (HA) species form so-called Harmful Algal Blooms (HABs), which can severely affect food web dynamics and interactions.

HABs appear in marine and freshwater ecosystems, where they can have deleterious effects on the ecosystem. In total, about 5000 marine phytoplankton species exist worldwide, but

only approximately 300 of them are known to form red tides (Hallegraeff, 2003; Sournia et al., 1991). Around 80 species produce toxins, which can accumulate or be transported to higher trophic levels, thus leading to contaminated shellfish and a poisoning of fish, marine mammals and humans (Hallegraeff, 2003). Also, some toxins can be transported with aerosols, leading to severe respiratory health issues of exposed humans (Cheng et al., 2005; Fleming et al., 2007). Fleming *et al.* (2007) showed that especially people with pre-existing asthma showed increased respiratory symptoms already after only 1h of exposure to aerosols of *Karenia brevis* during a bloom. HA toxins, depending on the type of toxin and the dosage can have dramatic effects on human health (Grattan et al., 2016; Yan and Zhou, 2004), and have thus been categorised after these effects (see Table 1). The strong threat to humans' health and the direct effects on other species through HAB outbreaks can lead to serious economic damage in fisheries and tourism causing high costs. Chile, the world's second largest salmon producer, has experienced devastating effects through HABs. In 2009, a massive bloom of *Alexandrium catenella* caused intense salmon mortality and led to a loss of $10M to the Chilean salmon industry (Mardones et al., 2010, 2015). As aquaculture operations will expand due to increasing human populations (Anderson, 2012), also increasing economic losses due to HABs in the future are likely, as they are especially vulnerable for such events. HABs and their versatile negative effects on the ecosystem and thus also on the economy have raised public concern and sparked several monitoring and modelling programs to improve the understanding of HAB dynamics (Anderson et al., 2015).

Factors influencing HABs

A strong interaction of chemical, physical and biological parameters shapes the occurrence of phytoplankton blooms, including HABs. Many of these biotic and abiotic factors are of natural origin, but can also be anthropogenically modified or introduced, such as enhanced nutrient loadings through agriculture (Fig.1; Anderson, 2012).

Table 1 Seafood intoxications of common HA toxins
*(modified after Grattan, Holobaugh and Morris Jr., 2016 and references therein); Abbreviated symptoms: **a**, allergic-like; **ab**, abdominal cramps; **b**, bronchoconstriction; **bp**, decrease in blood pressure; **d**, diarrhea; **n**, nausea; **p**, paresthesia; **r**, respiratory distress; **t**, reversal of temperature sensation; **v**, vomiting*

Syndrome	Major Toxin	Major Symptoms	Onset Time and Duration
Ciguatera Fish Poisoning (CFP)	Ciguatoxin	**n**, **v**, **d**, **ab**, **p**, **t**, **bp** Also: metallic taste, itching, dizziness. Possible recurrence of neurological symptoms during times of stress, after ingesting alcohol or low-level fish. Low mortality in the US.	12-24h; Neurological symptoms can last months to years
Diarrhetic Shellfish Poisoning (DSP)	Okadaic Acid	**d** (incapacitating), **n**, **v**, **ab** Headache, fever. No reported mortality.	30min - 15h; Full recovery within 3 days
Neurotoxic Shellfish Poisoning (NSP)	Brevetoxin	*Consumption*: **p**, **ab**, **t**, **d**, **b**, **r** (most severe cases). May appear disorientated or intoxicated (slurred speech, pupil dilation, overall fatigue, involuntary muscle spasms). *Inhalation*: **a**, **b**, **r**. Throat irritation, sneezing, coughing, itchy and watery eyes, burning of the upper respiratory tract. No reported mortality for either pathways.	*Consumption:* Few min - 18h *Inhalation:* Few min - hours (<24h)
Paralytic Shellfish Poisoning (PSP)	Saxitoxin	**p**, **n**, **v**, **r** (severe doses: respiratory paralysis and death). Muscular weakness, drowsiness, incoherent speech. No mortalities in the recent US and European outbreaks.	30min-3h; Few hours - few days
Amnesic Shellfish Poisoning (ASP)	Domoic Acid	**ab**, **n**, **v**, **r**, disorientation, seizures, permanent short-term memory loss, possible neurodevelopmental delay. Excessive respiratory secretions. Coma and death only among most severe cases or elderly	Within 48h; Months to years with permanent amnesia

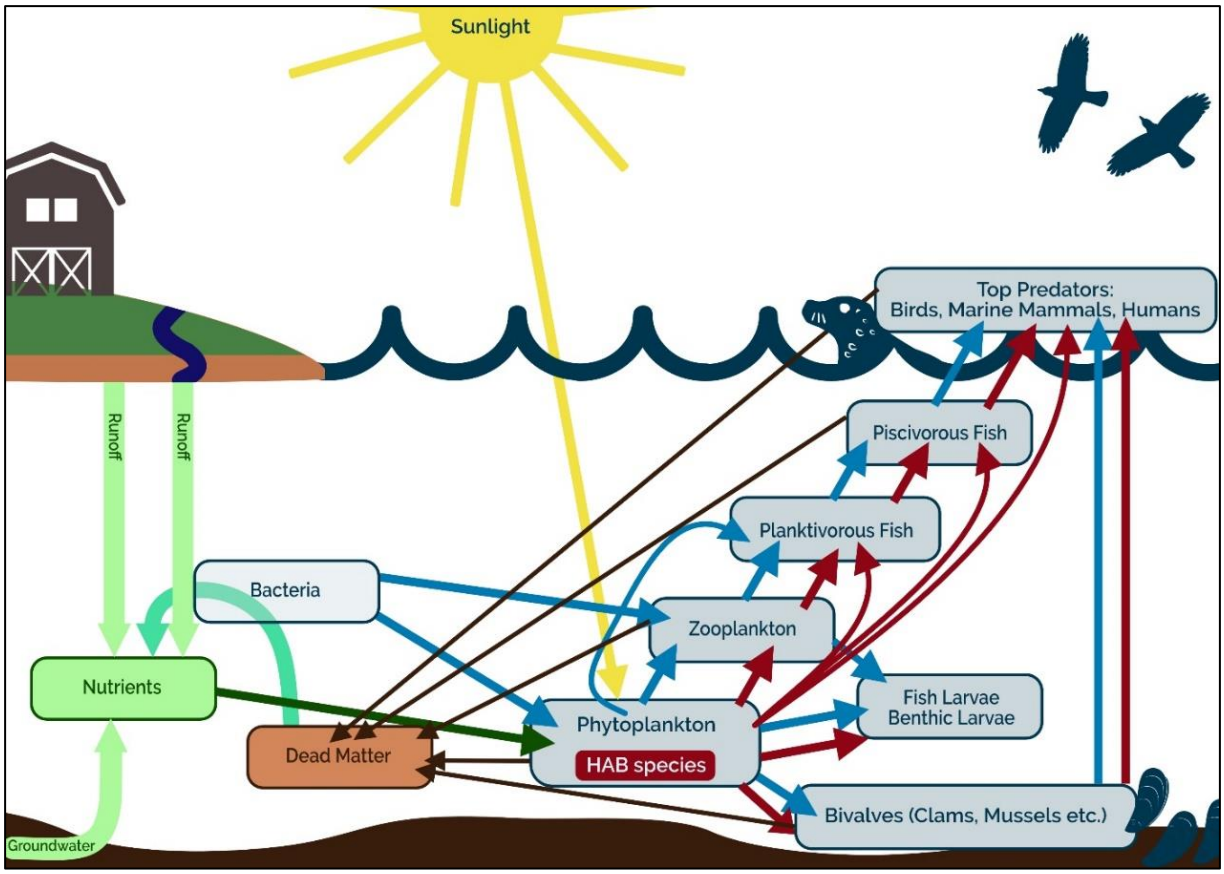


Figure 1 Conceptual model of the marine food web. The illustration shows the complexity and dependency of main groups within the marine food web. Sunlight, as well as natural and anthropogenic nutrient input, influences phytoplankton growth and thus food web dynamics. Harmful algal blooms can potentially influence all levels of the food web, due to the production of toxins, anoxic conditions, or their morphology (e.g. spines).

Harmful algal species have, similar to non-HA phytoplankton species, unique growth and living requirements and thus form blooms under a variety of conditions. Some species, for instance, thrive in low saline environments, such as estuaries, whereas other species require higher salinities (Kim et al., 2004; Taylor and Pollingher, 1987; Xu et al., 2017). Other factors, such as light, pH or nutrient availability can influence phytoplankton performance (Granéli and Turner, 2006; Kim et al., 2004; Sobrino et al., 2014; Xu et al., 2017). Organic and inorganic nutrients, including nitrogen and phosphorus, often underlie strong temporal and spatial fluctuations and are crucial for phytoplankton bloom development (Anderson et al., 2002; Bristow et al., 2017). Nutrients are naturally introduced into oceans via rivers and groundwater (Fig. 1). Runoff from urban and agricultural regions increases the input of nutrients into marine environments and can promote HAB formation (Anderson et al., 2002). In upwelling regions, nutrients from bottom waters, which have been reintroduced into the system through bacterial decomposition and remineralisation of dead matter, are transported into the

euphotic zone via upwelling waters (De La Rocha, 2003). Upwelling regions have been, due to their increased nutrient input, described as “hot-spots” for many phytoplankton species, including HA species (Martin and Richards, 2002; Pitcher et al., 2010).

In addition, biological factors, such as competition and predation are of essential importance for bloom dynamics of harmful algae (Chakraborty and Feudel, 2014; Vidal et al., 2017). Bloom formation and duration but also termination depends strongly on the ecology of the HAB species and its co-occurring organisms in the ecosystem. Competition between phytoplankton species for resources, such as light and nutrients, is a key ecological process, which shapes phytoplankton communities (Litchman, 2007). Different competition and interaction theories exist in community ecology, which have also been applied to HABs. In community ecology, the R* theory is a basic competition theory, which attempts to predict the outcome of competition for resources (Tilman, 1985, 1982). This model predicts, that if species are competing for a single limiting resource, the species that decreases resources to low levels and can survive under these low resource conditions (exhibits the lowest R*/ the lowest equilibrium resource level) will outcompete the other species. However, when competing for multiple resources, a trade-off in the ability to efficiently use different resources allows coexistence of competitors (Tilman, 1985, 1982). Margalef (1978) identified different taxonomic/functional phytoplankton group responses in a nutrient-turbulence space in his famous “mandala”. A conceptual approach, based on Grime (1977), which has been adapted to phytoplankton but also to HABs is Reynold’s C-S-R model (Reynolds, 1987; Smayda and Reynolds, 2001), which distinguishes between three different life forms: (C) the colonist, which is invasive, and small- to intermediate-sized; (S) the large and slow growing and stress-tolerant species; (R) and the ruderal cells, which are disturbance tolerant and can cope with high light and high nutrients. Such approaches help to describe and identify patterns of competition and interactions of communities.

Another factor, which can influence HABs is grazing. Grazing can either lead to the termination of a bloom through direct grazing on the HA species or even promote a bloom via a positive feedback loop through feeding on competing species, which results in a competitive release (Buskey, 2008; Smayda, 2002; Sunda et al., 2006). Community responses and hence HAB

success can be influenced by changes of all biotic and abiotic factors, demonstrating the complexity of bloom dynamics.

Characteristics of upwelling regions

Many highly productive regions, such as the Canary Current, the Benguela Current or the California Current, are upwelling systems (Fréon et al., 2009). These regions play an important role in the global fish market as they provide high fish and primary production (Fréon et al., 2009; Pauly and Christensen, 1995). Due to their high economic and ecological value, upwelling regions are thus especially vulnerable to the effects of HABs.

The combination of physical and geographical characteristics has a strong influence on nutrient supply and other factors such as temperature and salinity. Upwelling is caused by winds blowing across the sea surface, causing a strong wind-water interaction. The wind direction is crucial for the occurrence of upwelling events. If, for example, the wind blows south at the California Coast, it blows parallel to the coast where the Ekman transport moves the water 90 degrees to the side, thus leading to an offshore transportation of surface waters and an upward flow of deep cold and nutrient-rich waters to the surface (Fig. 2; Bakun 1990; Smith 1964). There are general circulation patterns in upwelling systems. However, upwelling dynamics are affected by the bathymetry, the continental shelf and the coastline morphology (Kudela et al., 2005). Upwelling circulations and thus wind, currents and water movement in general have been shown to be important for HAB retention, initiation and dispersion (Bialonski et al., 2016; Kudela et al., 2005; Pitcher et al., 2017, 2010).

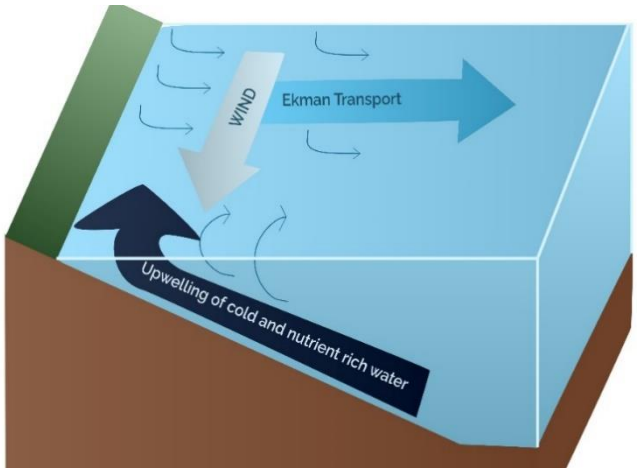


Figure 2 Coastal Upwelling: Wind blows parallel to the coast. Ekman transport moves surface waters from the coast off shore. Surface waters are replaced by cold and nutrient-rich water via upwelling

As upwelling is often seasonal, nutrients are not supplied throughout the whole year but in temporally limited pulses (Pitcher et al., 2010). Thus, the interplay of upwelling and relaxation periods promotes differently adapted phytoplankton species.

HAB and phytoplankton dynamics of the California Current Upwelling System

The California Current is a part of the eastern boundary current system, which moves southward along the northern American west coast between southern British Columbia in Canada and Baja California Peninsula in Mexico (Checkley and Barth, 2009; Fréon et al., 2009). This system belongs to the North Pacific Gyre which occupies large areas of the northern Pacific Ocean.

A variety of HAB events along the Southern Californian Coast have made this region a "hot-spot" for HAB research (Anderson et al., 2011; Bialonski et al., 2016). In upwelling regions, such as the Southern Californian Coast, some blooming patterns have recurred, emphasising a strong interaction between diatoms and dinoflagellates. Frequently occurring HAB species are diatoms of the genus *Pseudo-nitzschia,* where *P. australis* and *P. multiseries* represent the main domoic acid (DA) producers in California (Trainer et al., 2000). However, the most diverse HAB group occurring along the coast of California are dinoflagellates (Trainer et al., 2010). Since 2004, an increasing number of dinoflagellate bloom events have been recorded in California, including blooms of *Dinophysis* spp., *Alexandrium catenella Akashiwo sanguinea*, *Cochlodinium fulvescens* and *Ceratium sp.* (Howard et al., 2012; Matrai, 1986; SCCOOS, 2017). Upwelling events increase mixing and nutrient input and hence create an environment, where diatoms often bloom during, or shortly after (Margalef, 1978; Pitcher et al., 2010; Smayda and Trainer, 2010). In contrast, dinoflagellates have been found to bloom in relaxation periods, which are characterised by low mixing, low turbulence and a stronger stratification of the water column (Margalef, 1978; Pitcher et al., 2010; Pitcher and Nelson, 2006; Smayda and Trainer, 2010). In general, dinoflagellates exhibit lower growth rates than diatoms (Litchman et al., 2007). Margalefs mandala describes diatoms as the r strategists, and the dinoflagellates as K strategies (Glibert, 2016; Margalef, 1978). However, these groups can also be categorised after Reynold's C-S-R model, which includes habitat differentiation, and would classify diatoms between S and R strategists under high mixing, whereas dinoflagellates appear in all

categories (Smayda and Reynolds, 2001). However, dinoflagellates have a variety of traits, helping them to succeed under stratified and nutrient-depleted conditions. Many dinoflagellate species can take up nutrients through mixotrophic feeding on bacteria and phytoplankton (Smayda, 1997; Zhang et al., 2013). This trophic mode might not only enable them to take up nutrients in systems where dissolved nutrients are scarce but might also increase the competitive release through consumption of the competitor. Vertical migration, as a strategy to increase nutrient uptake from deeper waters, has been shown for many dinoflagellates (Peacock and Kudela, 2014). Especially in combination with the potential ability to store nutrients (Collos et al., 2004), this migration facilitates nutrient uptake from deeper waters during the night and still thrive in nutrient-poor surface waters of stratified regions during the day. Additionally, vertical migration can also decrease grazing pressure through spatial avoidance (Bollens et al., 2012).

Dinoflagellate blooms in the California Current System vary in their spatial and temporal occurrence, as well as in their duration and magnitude (Trainer et al., 2010). The dinoflagellates pursue different strategies to increase their competitive success. Some dinoflagellates produce toxins which often affect higher trophic levels such as fish, marine mammals or humans (Doucette et al., 2006; Durbin et al., 2002; Geraci et al., 1989; Turner and Tester, 1997). While toxins can strongly harm some zooplankton species, others are unaffected (Turner and Tester, 1997). As many toxins do not affect grazers directly, it is assumed, that toxin production did not evolve to repel grazers (Turner and Tester, 1997). However, apart from toxin production, some dinoflagellates produce allelopathic substances as secondary metabolites, which often have lytic effects and can harm survival, growth and reproduction of potential competitors and consumer (Granéli et al., 2008; Smayda, 1997). Through their lytic activity, cell membranes of other phytoplankton species, grazers or even fish gills can be perforated (Granéli and Hansen, 2006). However, for many species, allelopathic substances are still unidentified.

Akashiwo sanguinea, for example, has been associated with bivalve deaths though gill clogging and subsequent suffocation as well as massive seabird mortality events caused by a mixture of extracellular proteins which reduce the water-repellency of the birds feathers, leading to hypothermia (Jessup et al., 2009; Lassus et al., 2016; Lewitus et al., 2012; Phillips et al., 2011). *Cochlodinium* sp. for example, has been related to worldwide salmon death, yet the

mechanism or toxin which causes these effects are still unknown (Lewitus et al., 2012). Additionally, many of the mechanisms leading to HAB formation and demise at the Southern Californian Coast are still poorly understood

Spatial studies in HAB research

Spatial aspects are of fundamental interest in HAB research, as coastal propagation of HABs has a huge impact on the aquatic ecosystem. Therefore, a variety of different studies have been made in HAB research, where monitoring and modelling studies represent a large portion and are also often combined.

Models are an essential tool for quantitative forecasting of climate change effects on harmful algal blooms, and a great emphasis on HAB research should lay on its development and improvement (Wells et al., 2015). Many models are often based on existing monitoring HAB data, such as a study of Karki *et al.* (2018) who developed data-driven models which relied on field data and spatiotemporal remote sensing of 213 bloom events of *Karenia brevis* in coastal water of Charlotte County, Florida. By developing models for nowcasting and up to three-day forecasting of *K. brevis* blooms and their propagation, they identified chlorophyll a, euphotic depth, sea surface temperature, and some other factors, to be relevant for controlling HABs in this area (Karki et al., 2018). Bialonski *et al.* (2016) conducted a simulation study on the potential dependencies between environmental factors and HAB taxa and the influence of transportation via currents and local hydrography within the Southern California Bight. In their study, they found that transportation via currents is an important mechanism for the expansion and distribution of some taxa, whereas other phytoplankton taxa dynamics were linked to local environmental conditions, such as coastal upwelling (Bialonski et al., 2016). Chakraborty and Feudel (2014) developed a model to examine excitable dynamics of a system in which two different phytoplankton groups (non-toxic and toxic phytoplankton) compete for the same nutrients and where nutrient input and selective predation can alter bloom dynamics. They showed, that the toxic species gained a competitive advantage through nutrient enrichment and selective predation by zooplankton, thus indicating, that the interplay between competition, excitability and selective grazing pressure controls emergence and severity of HABs (Chakraborty and Feudel, 2014).

From these studies, it becomes apparent, that HABs are influenced by a combination of local environmental biotic and abiotic factors as well as spatial patterns. However, there is a lack of empirical studies including multiple factors. Especially manipulations of biotic and abiotic factors have not been done at different spatial scales.

Studies on large spatial scales often allow for dispersal of species, which can lead to an accumulation but also dilution of organisms. A tool to implement dynamics such as dispersal are meta-ecosystems. They are defined as sets of interconnected local patches or habitats, which are linked by the spatial flow of organisms, materials and energy, thus allowing the detection of complex population dynamics on different spatial scales (Loreau et al., 2003). Meta-ecosystem approaches have been established in other ecological fields to investigate the role of dispersal for ecological interactions and spatial dynamics of species. Such a meta-ecosystem approach, studying spatial dynamics and complex interactions of HABs, could reveal relevant influences through the manipulations of biotic and abiotic factors. However, until now, this method has not been applied in HAB research.

Aim of this thesis

Harmful algal blooms can have considerable effects on the marine food web. Thus it is important to understand their spatial and temporal population dynamics. While HABs have been studied intensively, most studies took a monitoring approach for potentially affected areas or focused on laboratory studies of biological properties of single HA species or single interactions. Monitoring field studies often cover large coastal areas and provide information on potential factors promoting bloom propagation. Laboratory studies, in contrast, allow direct manipulations and reveal more mechanistic and causal relationships between population dynamics and particular environmental factors. For example, influences on HABs, such as light, nutrients or pH have intensively been studied in the past (e.g. Kim et al., 2004; Laabir et al., 2011; Xu et al., 2017). However, complex HAB dynamics, including interactions with other community members or grazers in dependency of abiotic factors have not been studied. Hence, experimental manipulation of such factors in controlled laboratory experiments incorporating spatial properties is required to gain a broader understanding of the factors determining bloom formation and propagation.

The overall aim of this thesis was to investigate trophic interactions and propagation of potentially harmful dinoflagellates along environmental gradients in a spatial context. In order to increase the understanding of complex HAB dynamics on a spatial scale, I conducted two meta-ecosystem experiments and one batch experiment with the harmful dinoflagellates *Alexandrium catenella* and *Lingulodinium polyedra*, as they regularly occur in the Southern California coastal upwelling system. This study was the first approach to study the two different HA species in a spatial and controllable context, using a meta-ecosystem set-up.

In the **first Chapter,** I investigated ecological interactions and spatial dynamics of the toxic and allelopathic dinoflagellate *Alexandrium catenella*. I studied competition and propagation dynamics of *A. catenella* in a meta-ecosystem-setup in sets of five interconnected experimental flasks. To analyse interactions between nutrient distribution and propagation of *A. catenella*, flasks were either subject to a nutrient gradient or held equal nutrient concentrations. *A. catenella* was introduced into different positions, to investigate the importance of the inoculation position for the bloom development. Controls without *A. catenella* were set up to analyse the impact of *A. catenella* on the competing phytoplankton species. This meta-ecosystem experiment represents a novel approach in the context of HAB research. Based on these results I discuss the relevance of dispersal in combination with nutrient distributions and community dynamics for *A. catenella* bloom dynamics on two spatial scales.

The focus of **Chapter 2** was the investigation of bloom development of the harmful dinoflagellate *Lingulodinium polyedra* in dependence of its spatial and temporal introduction to the meta-ecosystem. *L. polyedra* was, similar to the experiment of Chapter 1, inoculated along a nutrient gradient into a meta-ecosystem. However, in contrast to *A. catenella*, *L. polyedra* does not produce allelopathic substances and might thus follow a different blooming strategy. As competitive interactions of the community might vary between the inoculation of *L. polyedra* at the beginning of the experiment and after a development phase of nine days, I analysed its successional dynamics and whether timing, and nutrient availability play a role in bloom establishment. To determine the effect of nutrient dynamics and inoculation position, *L. polyedra* was either added to the highest or the lowest nutrient concentration along the gradient.

In the first two studies (Chapter 1 and 2), which were carried out with phytoplankton communities assembled from laboratory cultures, I gained a better understanding of the underlying mechanisms how environmental factors determine population dynamics of the target dinoflagellates. However, in complex, natural communities, patterns might be different due to other interacting factors, such as the presence of multiple trophic levels and therefore higher grazing pressure and competition. In **Chapter 3**, I therefore studied bloom dynamics and persistence of *L. polyedra* in dependence of the timing and composition of nutrient pulses in natural phytoplankton communities from the Southern Californian coast. Thus, two experiments were conducted at the University of Southern California (Los Angeles) at the Caron Laboratory, using two different natural plankton communities off the coast of Los Angeles. Based on the results, I discuss the importance of community composition and grazing for bloom dynamics of *L. polyedra* and the predictability of general community dynamics.

Chapter 1

Competition and spatial dynamics of the harmful dinoflagellate *Alexandrium catenella* along a nutrient gradient: A meta-ecosystem study

Abstract

Harmful algal blooms (HABs) are increasing in number and spatial extent. However, their propagation dynamics along environmental gradients and the associated interplay of abiotic factors and biotic interactions are still poorly understood. In this study, a nutrient gradient was established in a linear meta-ecosystem setup of five interconnected flasks containing a phytoplankton community. I investigated dispersal and population dynamics of the harmful dinoflagellate *Alexandrium catenella*, which was introduced into different positions along the nutrient gradient. Limited daily dispersal was allowed to ensure species dispersal between the flasks, but to also maintain the nutrient gradient until the end of the experiment.

Overall, *A. catenella* was able to disperse through all flasks. Community composition and total biomass were highly influenced by the nutrient gradient, with increasing total biomass and decreasing community evenness at high nutrient concentrations. On the regional scale, diatoms dominated the community, whereas, on the local scale, the dinoflagellate showed higher contributions to total community biomass at lower nutrient concentrations after a decrease in diatom abundances. *A. catenella* even dominated the community at the lowest nutrient concentration when initiated into this flask. An additional control without dispersal revealed an even stronger dominance of *A. catenella* at the lowest nutrient concentration,

indicating that dispersal and its associated nutrient exchange may weaken dinoflagellate dominance under low nutrient conditions.

This study presents a first approach to investigate spatial dynamics and ecological interactions of a harmful dinoflagellate along an environmental gradient in a meta-ecosystem set-up, enhancing the understanding of the relevance of dispersal in combination with local environmental factors.

Introduction

Worldwide, harmful algal blooms (HABs) are increasing in number and in spatial extent, which can have severe negative impacts on coastal ecosystems, potentially leading to serious economic and ecological losses (Dyson and Huppert, 2010; Gibble et al., 2016; Horner et al., 1997; Trainer et al., 2000; Walz et al., 1994).

The term harmful algae covers a variety of species with different adverse effects, such as the production of toxins, which can accumulate and propagate up the food web, the emergence of anoxic conditions through the formation and decomposition of high-density blooms (Turley et al., 2010), or the physical damage of other species through morphological structures, such as spines which can clog fish gills (Yang and Albright, 1992). Harmful algae comprise a wide variety of different taxa; dinoflagellates, however, form the largest group of harmful algae (Smayda and Reynolds, 2003).

HAB formation and persistence depend on a variety of abiotic environmental factors, such as nutrient availability and composition (Anderson et al., 2002), light intensity (Wells et al., 2015) as well as on biotic factors such as competition (Granéli and Hansen, 2006) and grazing (Turner, 2006). HAB propagation and expansion on a regional scale is further determined by ocean currents, storms and other natural phenomena, such as upwelling events (Anderson, 2009). For instance, Pitcher et al. (1998) reported wind as the main driving force of HABs in upwelling systems. Upwelling systems are highly dynamic and subject to a strong variability of dissolved nutrient concentrations and ratios. Inorganic nutrients are crucial in shaping competition and therefore phytoplankton biomass and community composition. Nutrient availability in upwelling systems depends on a variety of factors, however mostly on water column stratification, upwelling frequency and intensity. The Southern California Coast

represents a coastal upwelling region belonging to the eastern boundary current system. In this system a variety of different HAB species frequently occur, varying in their spatial and temporal occurrence, as well as in their bloom duration and magnitude (Trainer et al., 2010). In addition to local environmental factors, Bialonski et al. (2016) provided evidence for the importance of hydrodynamic transport for the occurrence and propagation of HABs by relating the connectivity of different areas in the Southern Californian Bight to HAB dynamics.

Diatoms often bloom during or shortly after upwelling events, when mixing is high (Kudela et al., 2005; Margalef, 1978), while dinoflagellates appear in higher abundances when mixing decreases and stratification increases (Langlois and Smith, 2001). Thus diatoms, which generally exhibit higher growth rates than dinoflagellates (Litchman et al., 2007), appear to be better competitors for dissolved nutrient. Dinoflagellates, however, have evolved a variety of different adaptive strategies that enable them to increase their competitive strength and/or to decrease grazing pressure. For instance, the production of lytic allelopathic metabolites can reduce the survival, growth and reproduction of co-existing competitors and consumers leading to competitive release and/or decreased grazing pressure (Barreiro and Hairston, 2013; Granéli et al., 2008; Inderjit and Dakshini, 1994; John et al., 2014b; Tillmann and Hansen, 2009). In addition, mixotrophy, i.e. the combination of obtaining energy via photosynthesis and particle ingestion, can provide a competitive advantage over strictly phototrophic algae (e.g. Stoecker et al. 2006; Burkholder et al. 2008). Mixotrophy can also lead to the competitive release, directly through the ingestion of potential competitors for dissolved nutrients, and indirectly by complementing dissolved nutrients with particulate nutrients from ingested prey, which is especially relevant in nutrient-limited environments. Both allelopathy and mixotrophy have been proposed to potentially facilitate bloom development and persistence (Granéli and Hansen, 2006; Stoecker, 1999; Zhang et al., 2013). Furthermore, it has been shown that some dinoflagellates are able to store nutrients (e.g. Dagenais-Bellefeuille & Morse, 2013), which is especially relevant in systems with intermittent high nutrient variability, such as upwelling areas. All these adaptive strategies contribute to the competitive success of bloom-forming dinoflagellates, especially in nutrient-poor stratified coastal waters and highly dynamic upwelling regions.

Since more than a decade, an increasing number of dinoflagellate bloom events has been recorded in California, including blooms of *Alexandrium catenella Akashiwo sanguinea*,

Cochlodinium fulvescens, *Ceratium sp. a*nd *Dinophysis* spp.. Blooms of different species have been related to different factors. For instance, *Cochlodinium* sp. blooms have been related to increased inputs of nitrogen and a decrease in the surface water temperatures (Howard et al., 2012). However, many of the mechanisms leading to bloom formation and demise of different HAB species are still poorly understood.

Harmful events caused by *Alexandrium* sp., which produces saxitoxin, have increased in frequency and abundance along central and southern California (Jester et al., 2009b). Species of the genus *Alexandrium* produce saxitoxins, which are counted among the deadliest algal toxins (SCCOOS, 2017). Saxitoxins can cause mass mortality of fish, birds, and marine mammals due to the accumulation of the toxins within the food web (Cembella et al., 2002; Jester et al., 2009a; Lefebvre et al., 2016). Furthermore, they can lead to paralytic shellfish poisoning (PSP) outbreaks in humans through the consumption of contaminated seafood. Within the California Current system, *A. catenella* was found to be the dominant PSP-toxin producer (Trainer et al., 2010). This species is also able to produce allelopathic substances, harming potential competitors and consumers (Busch, 2016; John et al., 2014b; Tillmann et al., 2009; Tillmann and John, 2002), thus providing a competitive advantage for *Alexandrium*. It has also been shown to feed mixotrophically (Jeong et al., 2010, 2005a) and to be able to store nutrients (Collos et al., 2004), which might facilitate its dominance especially under nutrient-depleted conditions. However, the location, as well as the timing of these blooms have been highly variable, and their exact patterns, mechanisms and dynamics are still unclear (Moore et al., 2011).

To date, field studies on HABs often cover large spatial ranges as HABs can be transported along coastlines and along various physical and chemical gradients, along which plankton community composition and thus competitive interactions change, potentially also leading to changes in the competitive success of HAB species. Dispersal via ocean currents facilitates the propagation of HABs, while local environmental factors determine their competitive success and persistence. Field studies on HABs provide important information on which factors potentially promote bloom formation, propagation and demise. A deeper understanding of causal relationships between particular environmental factors and HAB population dynamics, however, requires manipulative experiments. Numerous laboratory studies analyzed the relevance of local environmental factors determining HAB dynamics, such as nutrient

concentrations, potential competitors, and consumers (e.g. Busch, 2016; Jeong et al., 2005a; Kardinaal et al., 2007; Magaña and Villareal, 2006). While laboratory studies help to elucidate the importance of local abiotic and biotic factors for particular HAB species, they are often only conducted with single species or clones, which exclude community interactions. Monitoring studies, in contrast, can identify spatial patterns, which can be related to biotic and abiotic factors. However, no manipulations are possible. Thus, the combination of both, i.e. the manipulation of biotic and abiotic interactions in a spatial context could help to identify factors influencing HAB dynamics. Consequently, the role of ecological interactions of *Alexandrium* sp. along spatial gradients of environmental factors is still not well understood.

Metacommunity and meta-ecosystem set-ups have widely been used to study the role of dispersal for ecological interactions and spatial dynamics of species. Metacommunities are defined as sets of local habitats or patches, which are linked via dispersal of potentially interacting species, while meta-ecosystems represent connected ecosystems which are linked by the spatial flow of materials, energy as well as the flow of organisms (Holyoak et al., 2005; Leibold et al., 2004; Loreau et al., 2003). Many studies used patches with discrete boundaries (Logue et al., 2011), however, in nature, environmental factors and biotic interactions mostly change along continuous spatial gradients. For example, Gülzow et al. (2019), used a set-up of five linearly interconnected patches to study the effects of gradually distributed nutrients on marine phytoplankton communities. Such metacommunity or meta-ecosystem setups, however, have to my knowledge, not been used so far to investigate spatial dynamics of HABs.

I aim to fill this void by investigating spatial dynamics and ecological interactions of a Californian strain of the harmful dinoflagellate species *Alexandrium catenella* along a gradient of dissolved inorganic nutrients. In this experiment, I inoculated a phytoplankton community representing four potentially co-occurring species of the Southern California Bight into linear connected meta-ecosystems. These systems were either set up with a nutrient gradient or with constant nutrient conditions as a control, with the same total amount of nutrients available at the regional scale, to investigate local and regional dynamics of *A. catenella* and general community dynamics. After an initial establishment phase of the phytoplankton, *A. catenella* was introduced into different positions of the meta-ecosystem to investigate its invasion success and its propagation patterns along the different nutrient regimes. Dispersal

among the flasks allowed *A. catenella* to invade all patches, enabling it to thrive in patches with most favourable conditions. In addition, controls without the addition of *A. catenella* and without dispersal (with and without *A. catenella*) were established for both nutrient regimes (constant and gradient) in order to investigate interactive effects of dispersal and nutrient regimes on *A. catenella* dynamics.

I tested the following hypotheses regarding general community dynamics (H1-H3) and particularly *A. catenella* bloom dynamics (H4-H6) at the local (a) and the (b) regional scale:

(H1) (a) At the local scale, total biovolume increases with increasing nutrient concentrations, while equal biovolume is found in meta-ecosystem patches without nutrient gradient.

(b) At the regional scale, there is no difference in total biovolume with or without a nutrient gradient, as the total nutrient amount is the same.

(H2) (a) At the local scale, evenness decreases with increasing nutrient concentrations, while equal evenness is found in meta-ecosystem patches without nutrient gradient. (b) At the regional scale, evenness is higher in meta-ecosystems containing a nutrient gradient, as increased heterogeneity of resources increases potential resource niches and thus diversity.

(H3) (a) At the local scale, dispersal enhances the similarity of communities in different patches regarding biomass and composition, while the exclusion of dispersal results in more distinct local communities, especially in patches differing in nutrient concentrations.

(H4) (a) At the local scale, low nutrient concentrations promote *A. catenella* biovolume contribution as opposed to high nutrient concentrations, as this dinoflagellate is a better competitor under low nutrient conditions.

(b) At the regional scale, *A. catenella* therefore also contributes more to total biovolume in meta-ecosystems containing a nutrient gradient compared to homogeneous nutrient conditions.

(H5) (a) At the local scale, *A. catenella* biovolume is higher in close proximity to its inoculation position, especially when inoculated under low nutrient concentrations in meta-ecosystems containing a nutrient gradient, while inoculation position does not affect *A. catenella* contribution in meta-ecosystems without nutrient gradient.

(b) At the regional scale, inoculation position affects *A. catenella* biovolume only in meta-ecosystems containing a nutrient gradient, increasing its total biovolume especially when inoculated under low nutrient concentrations.

(H6) (a+b) At the local and the regional scale, dispersal decreases *A. catenella* dominance, especially in patches with low nutrient concentrations, as dominant competitors and nutrients will be dispersed among the flasks.

Material & Methods:

Meta-ecosystem design

In the present study, I used a meta-ecosystem to investigate trophic interactions and propagation via dispersal of *Alexandrium catenella* along a nutrient gradient in comparison to a system with constant nutrient conditions. I conducted the experiment with a linear meta-ecosystem, similar to Gülzow et al. (2019) consisting of five interconnected flasks to simulate connected patches. For this system, 50ml Erlenmeyer flasks (DURAN), which were customized with glassy tube attachments on two sides, were connected with 6cm long silicon tubes (5 mm

Ø, TYGON). The connections between the flasks were kept closed with locking clips (Bevara, IKEA), while dispersal was allowed by opening those clips for 2 minutes daily. All meta-ecosystem sets were placed and fixed randomly on a shaking table (Laboshake, Gerhardt). Different dispersal times combined with different shaking speeds were tested prior to the experiment. This dispersal time of two minutes daily was chosen at 80 rpm to ensure dispersal of all species, also of non-motile species like diatoms, but at the same time keep the nutrient gradient over time. In order to investigate effects of dispersal, controls without dispersal were set up (with nutrient gradient only, as the closed intermediate position represent the constant nutrient controls), where clips remained closed throughout the entire experiment.

Algae cultivation and medium preparation

All taxa used in this experiment were isolated from the coast of Southern California (David Caron Laboratory, University of Southern California, Los Angeles, USA). Species from three different taxonomic groups were selected, differing in size, motility, nutrient requirements and thus competitive ability (Tab. 1); two diatoms, *Thalassiosira sp.* and *Leptocylindrus sp.*, the cryptophyte *Rhodomonas abbreviata*, and two dinoflagellates, the non-toxic *Prorocentrum micans* and the toxic *Alexandrium catenella.* John et al. (2014a) recently suggested renaming the *Alexandrium tamarense* species complex based on rDNA classifications. According to their study, the North American ribotype of *Alexandrium* would belong to group I, which was suggested to be renamed *A. fundyense.* To be consistent with previous studies (e.g. Fraga et al. 2015) I use the well-established name *A. catenella*. For simplification, however, I will hereafter refer to all species with their genus name only.

Species biovolume (μm^3) was used as a proxy for biomass and determined microscopically (Axiophot, Zeiss) by measuring the lengths and widths of 30 randomly chosen individuals for each species and calculating their biovolume according to specific geometrical shapes (Hillebrand et al. 1999). Prior to the setup of the experiment, initial cell concentrations (cells ml^{-1}) and accordingly the biovolume (μm^3 ml^{-1}) of all stock cultures were determined.

Table 1 List of species included in the meta-ecosystem. Biovolume (µm³ cells⁻¹) was calculated based on measurements of 30 randomly chosen individuals.

Species	Taxonomic group	Biovolume (µm³ per cell)	Grouped as
Alexandrium catenella	Dinophyceae	11388,09	harmful algae
Prorocentrum micans	Dinophyceae	9894,87	community species
Rhodomonas abbreviata	Cryptophyceae	273,81	community species
Thalassiosira sp.	Bacillariaphyeae	22312,48	community species
Leptocylindrus sp.	Bacillariaphyeae	1069,10	community species

Stock cultures of all phytoplankton species were maintained in f/2 medium (Guillard, 1975; Guillard and Ryther, 1962) that was prepared from 0.2µm-filtered and autoclaved North Sea water, which was taken from the Jade Bay (Wilhelmshaven, Germany). Cultures were non-axenic and kept in culture flasks (TC-Flasks T75, Sarstedt) in a constant environment of 18°C and a light intensity of 80 µmol m^{-2} s^{-1} in a 12:12h light: dark regime.

Prior to the experiment, five different culture media were prepared using sterilized North Sea water. Vitamins and trace metals were added according to the f/2 medium (Guillard, 1975; Guillard and Ryther, 1962). Nutrient compositions were adjusted to the Redfield-Brzezinski ratio (Brzezinski, 1985), increasing evenly from medium one (M1) to medium five (M5; Tab. 2). Seven days prior to the experiment, cultures were pre-incubated at intermediate nutrient concentrations (medium M3 Tab. 2), in order to prevent additional nutrient input to the experiment when adding the cultures, but at the same time allow algal growth within the pre-incubation time.

Table 2 Initial nutrient concentrations of the five different media. Nitrogen (N), Silicate (Si) and Phosphorous (P). All concentrations increased stepwise (in µmol L^{-1}) and were adjusted to the Redfield-Brzezinski ratio.

Medium	N (µmol L^{-1})	Si (µmol L^{-1})	P (µmol L^{-1})
M1	13.44	12.60	0.84
M2	50.08	46.95	3.13
M3	86.72	81.30	5.42
M4	123.36	115.65	7.71
M5	160.0	150.0	10.0

Experimental Design and Setup

The meta-ecosystems were divided into two systems: the nutrient gradient treatment ("NU_{grad}": M1 - M5, Tab. 2) and the constant nutrient treatment ("NU_{const}": M3, Tab.2). NU_{grad} treatments were filled from flask one to flask five with medium M1-M5 (Tab. 2), respectively, with increasing nutrient concentrations. NU_{const} treatments were filled with M3 only, which equals the intermediate medium of the gradient treatments. Thus, the NU_{grad} and the NU_{const} meta-ecosystems contained the same total amount of nutrients and only differed in the distribution of nutrients along the meta-ecosystem.

All flasks of both systems were inoculated with a phytoplankton community consisting of *Rhodomonas, Prorocentrum, Thalassiosira* and *Leptocylindrus* (Tab. 1). All algae were added in equal biovolume to compensate for major variances in cell sizes (evenness= 1). A total algal biovolume of $4x10^6$ μm^3 ml^{-1} was added to each flask, culture addition and medium summing up to a total volume of 55ml per flask. All flasks of all meta-ecosystems were sampled every 3rd day by removing 15% of the total volume (8.25 ml) of each flask. In order to replenish nutrients, 15% volume was replaced with the respective medium (M1 –M5, Tab. 2), resulting in a semi-continuous design. Locking clips were kept closed during the samplings to avoid mixing due to differences in the filling level.

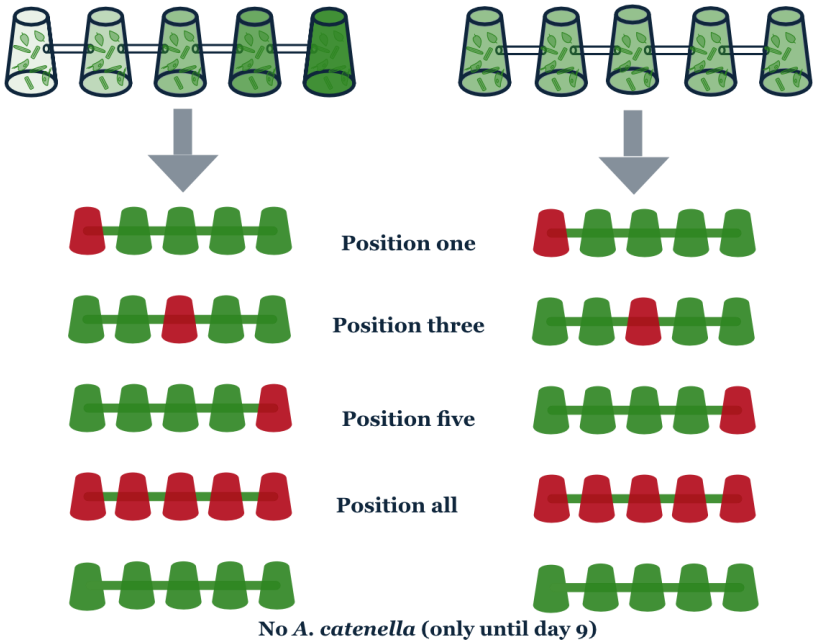


Figure 1 Setup of the meta-ecosystem experiment: The Nutrient gradient (on the left) increased stepwise N, P and Si concentration;, constant nutrient conditions (on the right) were filled with equal nutrient concentrations in all flasks; red flask represent the inoculation position of Alexandrium catenella

After an establishment phase of 9 days, to allow phytoplankton communities to develop according to different nutrient regimes, four treatments were set up, differing in the inoculation position of *Alexandrium.* The toxic dinoflagellate *Alexandrium* was either added into position one ($NU_{grad}1$, $NU_{const}1$), position three ($NU_{grad}3$, $NU_{const}3$), position five ($NU_{grad}5$, $NU_{const}5$) or in all positions ($NU_{grad}A$, $NU_{const}A$), resulting in a 4 x 2 factorial design, with three replicates for each combination at the meta-ecosystem level (24 meta-ecosystem) and 120 units total. Irrespective of experimental treatment, *Alexandrium* was inoculated with a total biovolume of 10^6 μm^3 ml^{-1} in each meta-ecosystem, i.e. this biovolume was either added to only one flask of the meta-ecosystem (treatments $NU_{grad}1$, $NU_{const}1$, $NU_{grad}3$, $NU_{const}3$, $NU_{grad}5$, $NU_{const}5$) or divided between the five flasks of the meta-ecosystem (treatments $NU_{grad}A$, $NU_{const}A$). The refill of the fresh medium was therefore adjusted at day 9, when *Alexandrium* was added to the flasks, to avoid exceeding the total volume of 55ml (4.88ml *Alexandrium* culture and 3.37ml Medium in all inoculation positions; only the $NU_{grad}A$ and $NU_{const}A$ treatment received 0.976ml of *Alexandrium* culture and 7.274ml Medium).

While all connections were open for two minutes every day to allow species to disperse between patches, an additional set of control experiments was set up (six months after the

initial experiment) in order to investigate the effect of *A. catenella* absence and the effect of dispersal within that system, using the same protocol as described before. For the NU_{grad} conditions, controls were therefore set up without dispersal with and without the addition of *Alexandrium* and with dispersal, but without the addition of *Alexandrium*. For the NU_{const} conditions, also a control with dispersal, but without the addition of *Alexandrium* was set up. However, no additional control without dispersal was set up, as the intermediate nutrient treatments (M3) that were set up without dispersal with and without *Alexandrium* for the NU_{grad} conditions were the same as they would have been in all flasks of the NU_{const} conditions and therefore served as control.

All treatments and controls ran for a total duration of 33 days. All meta-ecosystems were kept in a temperature constant climate chamber at 20 ± 2 °C. The light intensity averaged 85 µmol m^{-2} s^{-1} with a constant 12:12 day: night rhythm. Water temperature and light intensity were logged continuously using data loggers (Onset HOBO Pendant® data logger).

To follow phytoplankton population dynamics, communities were sampled every 3rd day.

Of the removed samples (15%, 8.25ml, see above), 3.25ml were used to measure in vivo Chlorophyll *a* with a Fluorometer (TURNER DESIGNS, AquaFluor™). Subsequently, the same samples were preserved with 10% Lugols iodine in amber glass bottles for microscopic cell counting. For the analysis of dissolved nutrients, 5 ml samples of each flask were taken, filtered through 0.2 µm cellulose acetate syringe filters (Chromafil CA 20/25, Macherey-Nagel) and stored at -20°C. Due to technical issues, however, all dissolved nutrient samples of this experiment were lost.

Sample analysis

Depending on the total cell concentration of each flask, subsamples ranging from 0.5ml to 3ml were used to determine algal biovolume and community composition. Subsamples were counted in Utermöhl sedimentation chambers under an inverted microscope (DM IL LED, Leica) at 100x magnification. A total of 300 – 400 cells were counted per sample in a minimum of 10 randomly chosen grids.

Statistical analyses

All statistical analyses and graphs were performed using R version 3.4.3 (R Core Team, 2017) and the following packages: vegan, ggplot2, lme4, grid, plyr, reshape, lattice, pbkrtest, boot, MuMin, and car.

I analyzed the data for the local patch level as well as for the entire meta-ecosystem, i.e., across all five patches (mean of each meta-ecosystem) of three different time points of the experiment; the time just before *Alexandrium* was introduced into the system (day 9), an intermediate sampling date, at which *Alexandrium* had the strongest impact (day 18), and day 33, the last sampling day of the experiment.

On the local scale, I tested the effects of nutrient conditions (position along the meta-ecosystem) and the distance to the inoculation position to identify treatment differences of *Alexandrium* on the total algal biovolume, evenness, and the contribution of *Alexandrium* for all three time points. I used a linear mixed model, using the "lme4" package, which is a robust method to estimate the linear mixed- effect model coefficients and bootstrapping procedures ("boot" package) for the calculation of confidence intervals. The model included the flask identity as a random factor to compensate for dependencies between the flasks via dispersal. To analyze the effects of the initiation position on the different response variables, I calculated the distance to the initial inoculation position for each patch and used this distance as a factor in the model. Analyses were conducted separately for the controls as well as for the different sets of meta ecosystems with and without a nutrient gradient (NU_{grad} and NU_{const}) since I tested the effect of the different positions in the model, which represents the nutrient gradient for NU_{grad} but constant nutrient conditions for NU_{const}. Data were transformed if residuals were distributed heterogeneously (Tab 3 AB). Nakagawa & Schielzeth (2013) described the calculation of marginal and conditional r-squared values ("MuMIn" package), which were followed, in order to assess the model fit. Results of the bootstrapping of the linear mixed model can be interpreted as significant results if their upper and lower values did not include zero. Controls without dispersal were not connected and therefore functioned as independent units. They were tested in a one-way ANOVA with the position as the explaining variable and the same response variables as the linear mixed model.

In order to test the effects of initiation position and nutrient conditions (gradient, constant) on the regional level on total algal biovolume, evenness and on the percentage of *Alexandrium*, two-factorial ANOVAs were conducted for the three time points and for the controls separately. I used a one-factorial ANOVA for the analyses of day nine, where I only tested the effect of nutrient conditions since the factor "initiation position" did not yet play a role. Data were transformed if homogeneity of variances and/or Gaussian distribution were not given (Tab 4). The regional analyses of the controls without *Alexandrium* were conducted with a non-parametric Kruskal-Wallis analysis since homogeneity of variances was not given for any of the time points.

Results

Local Analyses

Within the nutrient gradient (NU_{grad}) treatments, the flask position and thus the nutrient concentration level influenced all response variables at all time points analyzed. Total algal biovolume significantly increased with increasing nutrient concentrations in the meta-ecosystems subject to the nutrient gradient in systems with and without dispersal (Tab. 3B & Appendix Tab. 1 & 2), supporting hypothesis H1 (a). When dispersal was allowed, not only nutrients dispersed but also all species could propagate through the system and potentially reinvade communities. Thus, communities without dispersal were more distinct. When dispersal was possible, total biovolume and species composition became more similar, confirming hypothesis H3(a). This effect was particularly visible between the controls without *A. catenella* (App. Fig. 4 A, C).

After the inoculation of all phytoplankton species with an equal biovolume (evenness = 1), local evenness decreased within the first days of the experiment in all treatments. This decrease was accompanied by an overall strong increase in total biovolume, which was largely influenced by the rapid growth of the diatom *Thalassiosira* (Fig. 2, 3, 4, 5). It became the dominant species in almost all flasks and therefore strongly determined local chlorophyll *a* and total biovolume patterns. Consistent with hypothesis H2 (a), local evenness decreased with increasing nutrient availability in the NU_{grad} treatment (Tab. 3B).

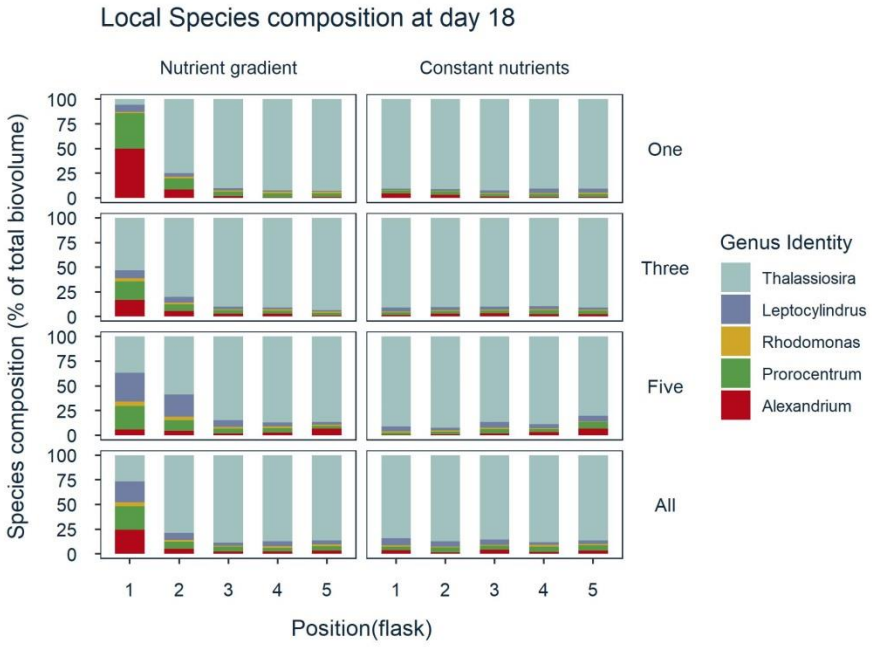


Figure 2 *Local species composition (as percentage of the total biovolume) at day 18. Results of the different A. catenella initiation positions (one, three, five, all) are shown. Within the nutrient gradient (NU_{grad}) treatments, position 1 represents the lowest, position 5 the highest nutrient concentration.*

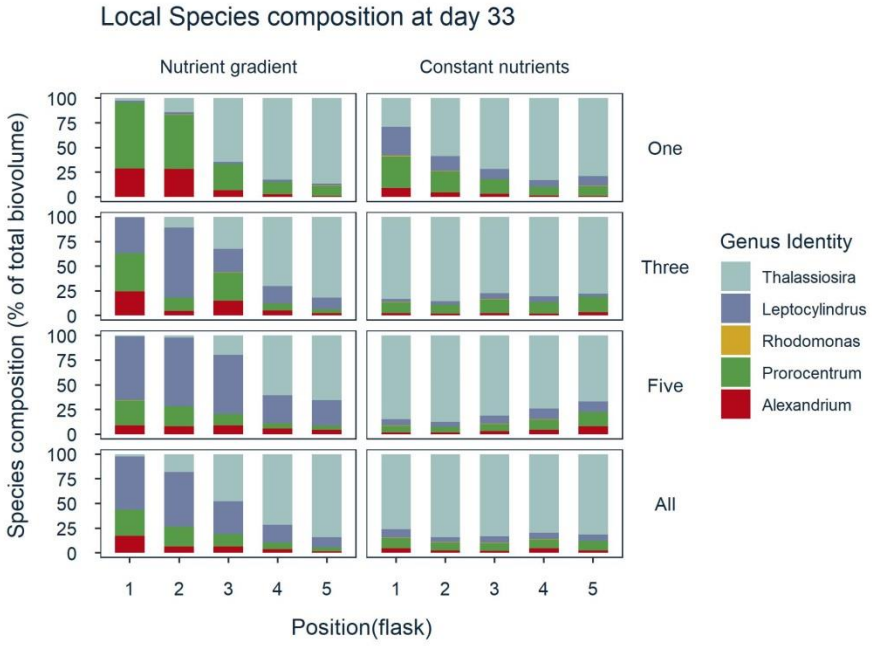


Figure 3 *Local species composition (as percentage of the total biovolume) at da 18. Results of the different A. catenella initiation positions (one, three, five, all) are shown. Within the nutrient gradient (NU_{grad}) treatments, position 1 represents the lowest, position 5 the highest nutrient concentration.*

After the introduction of *Alexandrium*, a significantly positive relationship between the distance of the inoculation patch of *Alexandrium* and the total algal biovolume was found for both, the NU_{const} and the NU_{grad} treatment, i.e. total algal biovolume was lower in flasks closer to the inoculation patch of the harmful dinoflagellate. However, this relationship was only significant on day 33, (Tab. 3, App. Fig. 8, 11). Across the nutrient treatments and all different initiation positions, the relative biovolume of *Alexandrium* always remained significantly higher closer to the initial inoculation position (Tab. 3), confirming hypothesis H5(a). The NU_{const} treatment allowed us to observe direct effects of Alex on other phytoplankton species without the interaction of altered nutrient supply in different flasks (NUgrad). I found species-specific differences in the NU_{const} treatments after the inoculation of *Alexandrium*. While *Prorocentrum* biovolume did not differ between local flasks, *Rhodomonas* showed the strongest reaction to the *Alexandrium* introduction and decreased drastically in high *Alexandrium* biomass patches (data not shown).

Both diatom species showed a small decrease in biovolume in those patches where *Alexandrium* was introduced (Fig. 2, 3), resulting in a significant increase in evenness closer to the inoculation position of *Alexandrium* (for day 18 and 33 in the NU_{const} treatment, and day 33 in the NU_{grad} treatment (Tab. 3A&B). However, also under lower nutrient concentrations in the NU_{grad} treatment, diatom dominance was reduced, and evenness significantly increased (Fig. 2, 3, Tab. 3B), whereas evenness remained lower in controls without *Alexandrium* addition (Fig.5A).

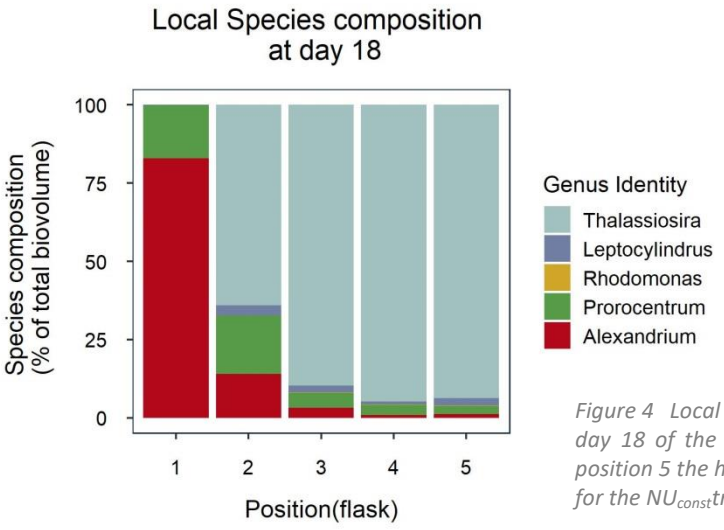


Figure 4 Local species composition (as percentage of the total biovolume) at day 18 of the control without dispersal. Position 1 represents the lowest, position 5 the highest nutrient concentration. Position 3 represents the control for the NU_{const} treatments.

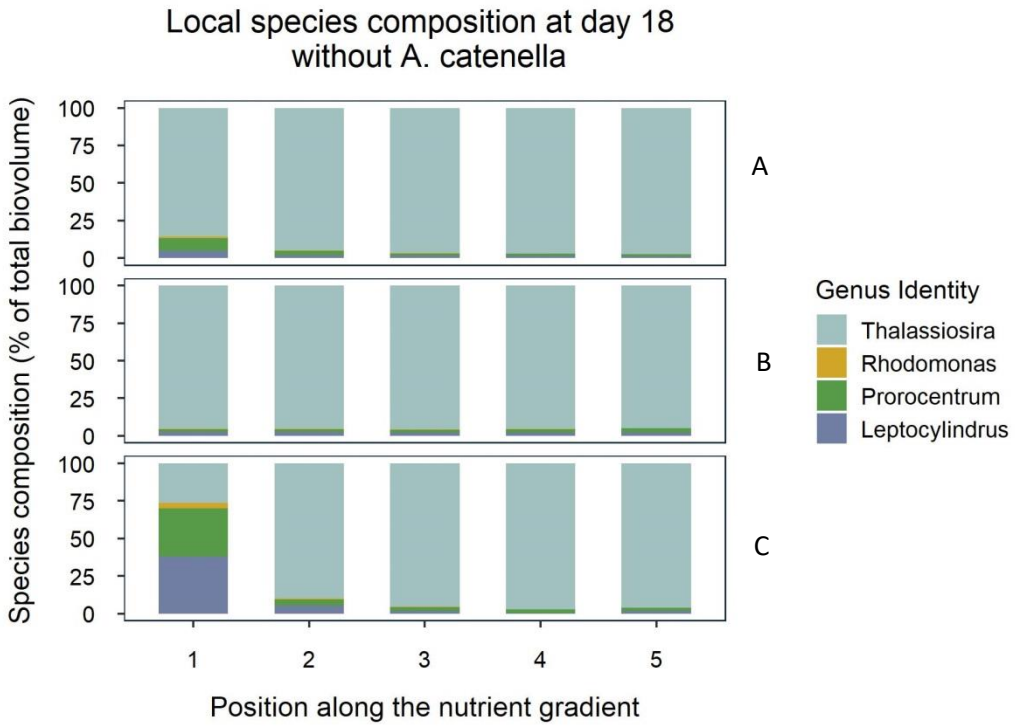


Figure 5 A,B,C *Local species composition (as percentage of the total biovolume) at da 18 of the control without A. catenella addition. A Control with dispersal for NU_{grad} treatment, where position 1 represents the lowest, position 5 the highest nutrient concentration. B Control with dispersal for $NU_{const,}$ where position 1 represents the lowest, position 5 the highest nutrient concentration. C Control without dispersal. Position 1 represents the lowest, position 5 the highest nutrient concentration. Position 3 represents the control for the NU_{const}treatments.*

Contributions of *Alexandrium* significantly increased with decreasing nutrient concentrations within the NU_{grad} treatments at day 18 as well as at day 33 (Tab. 3B, Fig. 2,3), confirming hypothesis H4(a). The highest relative biovolume of *Alexandrium* in treatments with dispersal reached almost 50% of the total algal biovolume at day 18 in the lowest nutrient concentration of the NU_{grad} treatments, where *Alexandrium* was initially inoculated (initiation position: one; Fig. 2). In the NU_{grad} treatments without dispersal, *Alexandrium* became even more dominant under lowest nutrient concentration, contributing more than 75% to total algal biovolume (Fig 4), supporting hypothesis H6. While *Alexandrium* mostly increased evenness, through the reduction of the great dominance of *Thalassiosira,* it decreased the evenness in this patch under the lowest nutrient conditions, due to the extinction of *Thalassiosira*. Additionally, also *Leptocylindrus* and *Rhodomonas* decreased to extremely low numbers.

Table 3 A & B *Results of local analyses of total biovolume, evenness and percentage of A. catenella of day 9, 18 and 33 from bootstrapping of the linear mixed model. If upper and lower values exclude zero, the result can be interpreted as significant (indicated by bold numbers). The factor "distance" is a measure for the distance to the inoculation patch of A. catenella at day 9.* ***A*** *Results for the constant nutrient (NU_{const})treatments, where the factor "position" represented equal nutrient conditions.* ***B*** *Results for the nutrient gradient (NU_{grad})treatments, where the factor "position" represented different nutrient stages along the nutrient gradient.*

A

Constant nutrient analyses of the LMM & Bootsrapping

Response	Day	Transformation	Coefficient	Estimate	Confidence interval		R^2 marginal	R^2 conditional
Biovolume	9	none	Position	71394	-1910193	2141408	0.000	0.026
	18	none	Distance	1751472	-7174	3653221	0.072	0.342
			Position	1017880	-2575694	453240		
	33	none	Distance	1131367	**901784**	**1367013**	0.680	0.827
			Position	170370	-12945	358801		
Evenness	9	none	Position	0.000	-0.009	0.010	0.000	0.086
	18	none	Distance	-0.020	**-0.037**	**-0.002**	0.077	0.365
			Position	0.005	-0.009	0.020		
	33	none	Distance	-0.073	**-0.094**	**-0.053**	0.327	0.767
			Position	-0.003	-0.018	0.012		
Percentage of *A. catenella*	18	log + 1	Distance	-0.307	**-0.385**	**-0.238**	0.548	0.642
			Position	0.044	-0.018	0.103		
	33	none	Distance	-1.329	**-1.745**	**-0.895**	0.335	0.638
			Position	-0.073	-0.384	0.256		

B

Nutrient gradient analyses of the LMM & Bootsrapping

Response	Day	Transformation	Coefficient	Estimate	Confidence interval		R^2 marginal	R^2 conditional
Biovolume	9	none	Position	15393427	**12855272**	**17890230**	0.665	0.745
	18	log	Distance	-0.059	-0.166	0.043	0.463	0.766
			Position	0.445	**0.356**	**0.527**		
	33	log	Distance	0.103	**0.009**	**0.198**	0.680	0.827
			Position	0.559	**0.485**	**0.635**		
Evenness	9	log	Position	-0.301	**-0.364**	**-0.238**	0.529	0.648
	18	none	Distance	0.027	-0.004	0.057	0.494	0.676
			Position	-0.117	**-0.144**	**-0.092**		
	33	none	Distance	-0.045	**-0.075**	**-0.018**	0.280	0.556
			Position	-0.057	**-0.079**	**-0.033**		
Percentage of *A. catenella*	18	log	Distance	-0.379	**-0.552**	**-0.203**	0.495	0.612
			Position	-0.529	**-0.671**	**-0.382**		
	33	log	Distance	-0.352	**-0.488**	**-0.232**	0.544	0.767
			Position	-0.514	**-0.621**	**-0.416**		

Regional Analyses

While local community and *Alexandrium* dynamics were clearly affected by the different initiation positions of *Alexandrium,* these differences could not be observed on the regional scale, where, responses were averaged over all five flasks of the meta-ecosystems.

After experimental setup, total algal biomass increased in all treatments up to day 6, after which both, algal biovolume and accordingly chlorophyll *a* slowly decreased. Total algal biovolume showed no significant differences between the NU_{grad} and the NU_{const} treatment of the controls without *Alexandrium* throughout the entire experiment, supporting hypothesis H1(b). However, for treatments with *Alexandrium,* I found a significantly higher total algal biovolume in the NU_{const} treatments compared to the NU_{grad} treatment for day 18 only ($p<0.01$, Tab. 4, Fig. 6, 7). This was in contrast to my expectations, that total algal biovolume would not differ between the nutrient treatments due to the equal total nutrient concentrations. Based on the overall regional results, I have to reject hypothesis H1(b).

The overall high local impact of *Thalassiosira* was also reflected in regional dynamics, showing a strong dominance of this diatom across the meta-ecosystems throughout the entire experiment (Fig 8). As a result, regional evenness was generally very low but slightly increased at the end of the experiment. I expected regional evenness to be higher in NU_{grad} meta-ecosystems (hypothesis H2(b)), as increased heterogeneity of resources increases niche availability, thus promoting species coexistence. In contrast to my expectation, regional evenness was significantly higher in the NU_{const} meta-ecosystems compared to the NU_{grad} treatments at day 18 and 33 ($p < 0.05$, Tab.4). However, this was only the case, when *Alexandrium* was inoculated at day 9. Thus, I can reject hypothesis H2(b), even though the controls without A*lexandrium* showed no differences between both nutrient regimes.

Figure 6 Mean regional total biovolume ± SE and mean chlorophyll a content ± SE in the NU_{const} treatments, split up into the different inoculation positions of A. catenella; Initiation in position one: A, Initiation in position three: B, initiation in position five: C, initiation in all flasks: D.

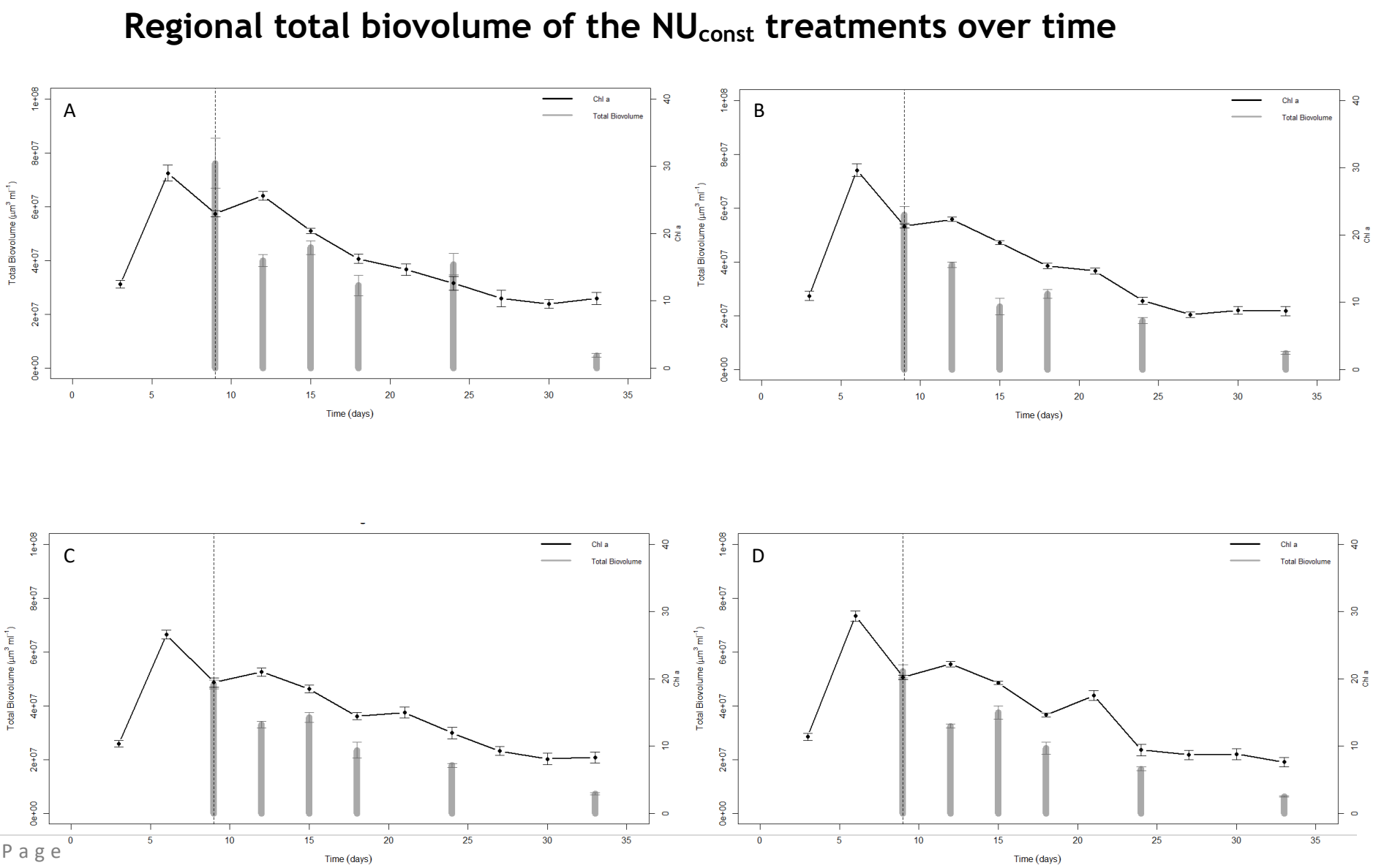
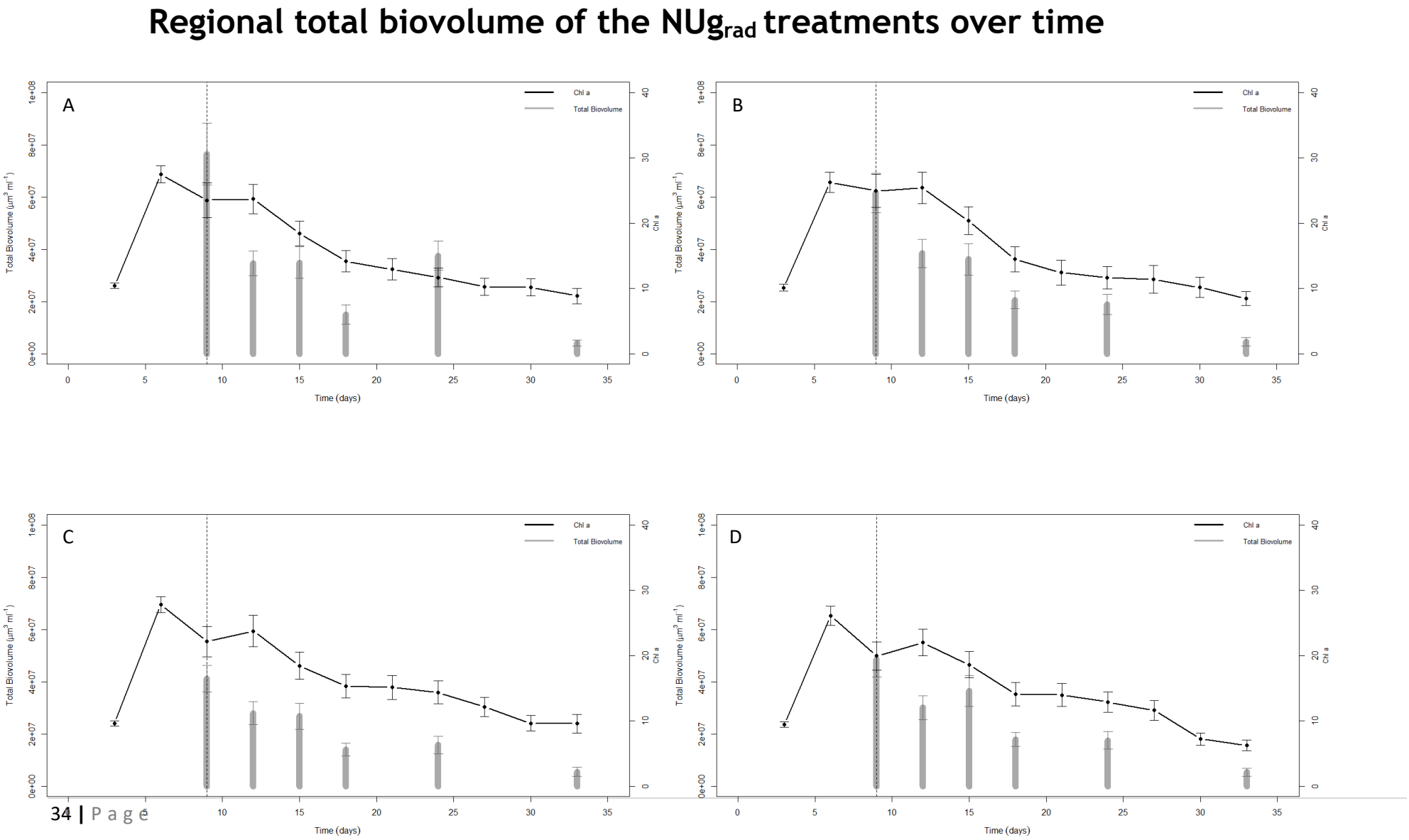


Figure 7 Mean regional total biovolume ± SE and mean chlorophyll a content ± SE in the nutrient gradient (NU_{grad}) treatments, split up into the different inoculation positions of A. catenella; Initiation in position one: A, Initiation in position three: B, initiation in position five: C, initiation in all flasks: D.



Alexandrium was expected to be a better competitor under lower nutrient concentrations, especially when initiated under these conditions (hypothesis H4(b)). I, therefore, expected to find higher *Alexandrium* contributions in the NU_{grad} treatments, compared to the NU_{const} treatments (hypothesis H5(b)). However, relative regional biovolume of *Alexandrium* was even higher in the NU_{const} treatments at day 18 and day 33 compared to the NU_{grad} treatments ($p<0.05$, Tab.4), hence rejecting hypothesis H4(b) and H5(b). While relative biovolume of the dinoflagellate was overall very low and did not change much over time on the regional scale, total biovolume of *Alexandrium* showed more variations. It slightly increased after inoculation at day 9, when inoculated into position one and five, reaching the highest biovolume at day 15 (Fig. 8). When *Alexandrium* was inoculated into position three and into all positions at the same time, both treatments (NU_{grad}, NU_{const}) showed no increase in *Alexandrium* biovolume (Fig 8).

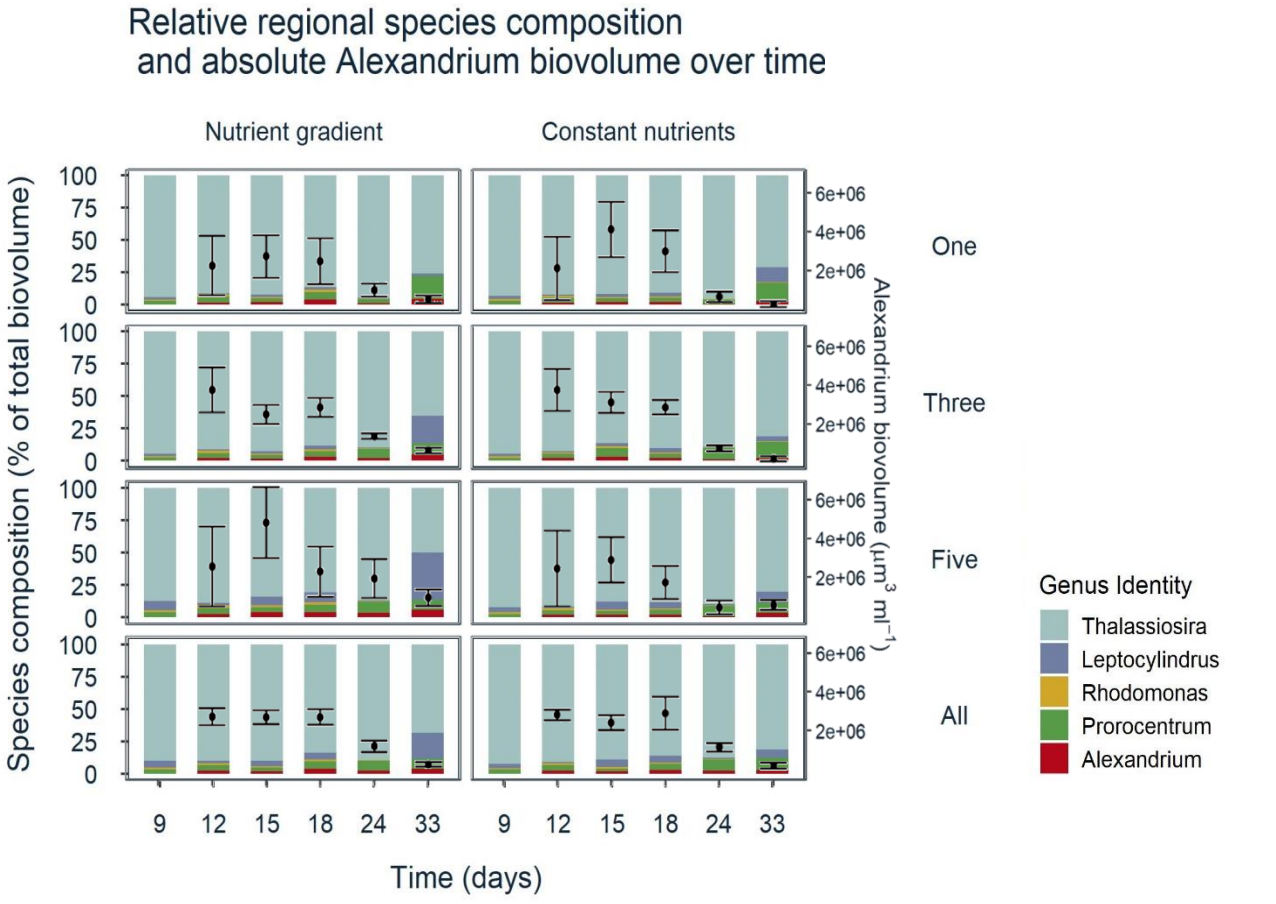


Figure 8 Regional species composition (as percentage of the total biovolume) and mean A. catenella biovolume ± SE (µm ^{3} ml $^{-1}$) over time. Results of the different A. catenella initiation positions (one, three, five, all) are split ups

*Table **4** ANOVA results of day 9, 18 and 33 for the analyses of regional total biovolume, evenness and percentage of A. catenella*

ANOVA results

Response	Day	Transformation (lambda)	Coefficient	dfN	F value	P value
Biovolume	9	0.61	Gradient	1	1.960	0.175
			Residuals	22		
	18	0.9	Initiation position	3	0.584	0.634
			Gradient	1	9.782	**0.006**
			Initiation position * Gradient	3	0.455	0.718
			Residuals	16		
	33	0.58	Initiation position	3	0.539	0.662
			Gradient	1	2.503	0.133
			Initiation position * Gradient	3	0.082	0.969
			Residuals	16		
Evenness	9	-0.88	Gradient	1	0.971	0.335
			Residuals	22		
	18	-0.52	Initiation position	3	1.529	0.245
			Gradient	1	4.807	**0.044**
			Initiation position * Gradient	3	0.197	0.897
			Residuals	16		
	33	-0.34	Initiation position	3	0.251	0.859
			Gradient	1	7.172	**0.017**
			Initiation position * Gradient	3	2.208	0.127
			Residuals	16		
Percentage of *A. catenella*	18	-0.88	Initiation position	3	0.298	0.826
			Gradient	1	8.798	**0.009**
			Initiation position * Gradient	3	0.578	0.638
			Residuals	16		
	33	-1.33	Initiation position	3	0.362	0.781
			Gradient	1	7.039	**0.017**
			Initiation position * Gradient	3	0.241	0.867
			Residuals	16		

Discussion

Overall, my meta-ecosystem experiment revealed complex regional and local distribution patterns of the harmful dinoflagellate *Alexandrium* in relation to nutrient availability and interactions with other phytoplankton species. *Alexandrium* was able to disperse quickly between all connected patches, demonstrating the applicability of this meta-ecosystem setup to investigate spatial dynamics of this species, and showing that this harmful alga was able to invade all of the differently shaped phytoplankton communities. Despite partly low concentrations, *Alexandrium* persisted in all flasks until the end of the experiment. Its relative biovolume contributions were strongly determined by nutrient concentration, its own initiation position, as well as community dynamics, especially the demise of the diatom bloom. Thus, I exhibited the highest contribution to total algal biovolume at low nutrient concentrations and closest to the inoculation position. In addition, dispersal appeared to counteract the *Alexandrium* bloom, as its dominance was much stronger under lowest nutrient conditions without dispersal.

Local dynamics

On the local scale, total algal biovolume significantly increased with increasing nutrient availability as expected. Diatom biovolume most strongly increased with nutrient enrichment, leading to a high dominance of diatoms, mainly of *Thalassiosira* sp., especially at intermediate to high nutrient concentrations. Diatoms often have higher maximum uptake rates of nutrients compared other phytoplankton groups as well as high maximum growth rates, which makes them generally good nutrient competitors (Litchman et al., 2007, 2006). Hence, they often benefit from turbulent waters, such as upwelling systems, where nutrients, but especially silicate concentrations are high (Margalef, 1978; Smayda, 1997; Seubert *et al.*, 2013). They can, therefore, become dominant and outcompete other groups like dinoflagellates, which are weaker competitors at high nutrient conditions (Margalef, 1978) and additionally, exhibit a lower growth rate than diatoms (Furnas, 1990; Smayda, 1997). In my experiment, the rapid growth of *Thalassiosira* was followed by a steady decrease of biovolume when nutrients became deplete, and the community structure changed and other phytoplankton species increased in proportion, especially the dinoflagellates *Alexandrium* and *Prorocentrum*, in particular under low nutrient concentrations.

Overall, *Thalassiosira* was prevalent at higher nutrient concentrations, whereas *Alexandrium* was more dominant at the lowest nutrient concentration. In a nitrogen-depleted environment, *Alexandrium* could have an advantage, due to its ability to accumulate and store nitrogen (Collos et al., 2004). Additionally, its ability to feed mixotrophically on other phytoplankton might be beneficial under low nutrient conditions in general and thus promote this dinoflagellate. In a pre-experiment, *Alexandrium* ingested cells of *Rhodomonas.* As the results showed that *Rhodomonas* decreased, when *Alexandrium* biomass was high, this reduction could have been caused by mixotrophic feeding, or the production of allelopathic substances.

While *Alexandrium* biomass slightly increased in the beginning, it decreased towards the end of the experiment. However, their relative contribution over time increased much stronger than their absolute biomass. Dinoflagellate contributions to total phytoplankton biomass highly depended on growth and the proportion of the diatom *Thalassiosira*. These results are in agreement with observed spatial and temporal patterns in the field. Anderson et al. (2008) showed that in the California bight (Santa Barbara channel) diatoms dominated the community in seasonally stratified and nutrient-rich surface water, especially after upwelling events. After nutrient depletion and stabilization of the water column, dinoflagellates became the dominant group in the community (Anderson et al., 2008). These temporal dynamics of a diatom bloom which is followed by a dinoflagellate bloom is a common phenomenon that was also observed in other habitats like, e.g. the Bornholm Basin (van Beusekom et al., 2009) or Georges Bank (Gettings et al., 2014). This pattern can be found on temporal scales of nutrient dynamics, but also on spatial scales. For instance, Mercado et al. (2014) studied phytoplankton community composition in the northwestern Alboran Sea (Western Mediterranean Sea), where a strong decreasing gradient of nutrients and chlorophyll can be found from the coast to offshore. In this area, they found coastal surface waters to be dominated by (<50 µm) diatoms, whereas offshore communities were dominated by dinoflagellates. This change in dominance from the coast to offshore was caused mainly by the decrease in diatom biomass, resulting in an increase of dinoflagellate biomass contribution to the total phytoplankton biomass (Mercado et al., 2014).

Dispersal in my experiment connected a heterogeneous or homogenous landscape and thus allowed *Alexandrium* to propagate through the system. Dispersal of *Alexandrium* was an

important factor shaping phytoplankton community structure. Although *Alexandrium* dispersed into all flasks within the first few days, independent from the inoculation position, the relative abundance of *Alexandrium* was always higher closer to its own inoculation patch throughout the entire experiment. This indicates that the initiation position of a HAB species might also be important in determining its dominance in a natural environment.

Coastal ecosystems are shaped by hydrodynamic characteristics such as currents, which play a crucial role in the propagation of phytoplankton in natural systems. Bialonski et al. (2016) showed in a study on the connectivity of different areas in the Southern Californian Bight, that when HABs were transported into new habitats, their success depended on the local environmental conditions. In my experiment, nutrients strongly shaped local conditions, however, also other environmental factors can influence habitats. Thus both abiotic factors such as nutrients, light and temperature, but also biotic interactions like competition and grazing can thus influence HAB invasion, persistence but also termination.

While dispersal ensured propagation of species and therefore maintained species diversity, my experiment showed that dispersal could weaken bloom formation. *Alexandrium* became much more dominant at low nutrient concentrations in the controls without dispersal compared to treatments, where dispersal was possible. However, I only tested one dispersal time. A higher or lower dispersal rate might lead to a different outcome.

In treatments with dispersal, not only algal species could disperse from other patches, but also nutrients were re-introduced into the patch with the lowest nutrient concentrations, which promoted diatom growth. In all treatments that included dispersal, all species survived in all flasks. However, the lack of dispersal led to lower biomass and finally the extinction of *Thalassiosira*, and a strong decrease of *Leptocylindrus* and *Rhodomonas,* especially at the lowest nutrient concentrations. These conditions enabled *Alexandrium* to outcompete diatoms and to become dominant. My results that species went extinct when dispersal of the heterogeneous landscape was removed are in accordance with the habitat heterogeneity hypothesis of MacArthur & MacArthur (1961). Heterogeneous landscapes provide more refuge spaces and lead to competitive avoidance. Thrush et al. (2013) showed in a defaunation

experiment with macrobenthos communities that recovery was influenced by local habitat features as well as by regional connectivity. For my experiment, I assume, that recolonization, even if species temporarily got extinct, was possible through the connectivity of those local patches.

As *Thalassiosira* dominance decreased with decreasing nutrient concentrations, community evenness increased. Due to the intermediate nutrient concentrations in the NU_{const} treatments, *Thalassiosira* was not able to increase in biomass as much as under high nutrient conditions of the NU_{grad} treatment, where it substantially decreased community evenness. While total algal biovolume decreased, evenness increased closer to the inoculation patch of *Alexandrium.* Mixotrophy and allelopathy are specific traits of *Alexandrium* that potentially promote its success under low nutrient conditions. The former might allow them to use nutrients derived from phagotrophy on bacteria or small phytoplankton, which are unavailable for the diatoms, the latter might affect the growth rate of the competitors negatively. In a pre-experiment, I tested the mixotrophic capability of *A. catenella* on the other phytoplankton species used in this experiment. While *Alexandrium* was able to ingest the cryptophyte *Rhodomonas*, it did not ingest the other, larger species. Other studies also showed mixotrophic feeding of *A. catenella* on different prey species, such as *Ostreococcus* sp. and *Synechococcus* sp. (Busch, 2016; Jeong et al., 2005b). However, also other environmental factors can influence mixotrophy. Legrand et al. (1998), showed that mixotrophic feeding of the dinoflagellate *Heterocapsa triquetra* only appeared under nutrient limitation but was additionally promoted in the dark, indicating, that other environmental factors can also influence mixotrophy.

Blossom et al. (2012) studied the prey uptake of *Alexandrium pseudogonyaulax*, which ingests cells after catching and immobilizing these prey cells through the secret of a toxic mucus trap. In this study, they also studied the mixotrophic capabilities of *A. catenella* and *A. minutum* for comparison and found no mixotrophic feeding of any of these strains on multiple different prey species, such as *Heterocapsa rotundata*, *Teleaulax acuta* and *Scripsiella trochoidea*. Their experiment, however, was conducted with sufficient nutrients, which would support the findings of (Legrand et al., 1998) that nutrient availability may determine mixotrophic-feeding activity. In my experiment, mixotrophic feeding activity might have been stronger under low

nutrient conditions of the NU_{grad} treatment compared to flasks with higher nutrient amounts. However, this is only speculative, as mixotrophy was not quantified in this study.

While I did not find mixotrophic feeding on the diatoms in my pre experiments, I found a decrease of both diatom species in patches where *Alexandrium* was added. In addition, the comparison between the different inoculation positions with the *Alexandrium* free control shows a clear reduction of the diatom dominance through *Alexandrium* introduction, again preferably under lower nutrient conditions. This might be an indication of allelopathic effects of *Alexandrium*.

A. catenella was shown to produce allelopathic substances, which can affect other species in different ways, as the compounds can reduce survival, growth and reproduction of competitors and consumers (Arzul et al., 1999; Barreiro and Hairston, 2013; Granéli et al., 2008; Inderjit and Dakshini, 1994; John et al., 2014b; Tillmann and Hansen, 2009). These lytic effects on other phytoplankton species are highly variable, even within strains of the same species (Blossom et al., 2012; Tillmann et al., 2009). Busch (2016), found an effect concentration (EC_{50}) of 566 cells ml^{-1} of the same *A. catenella* strain, as I used in my experiment for cell lysis of 50% of the target cell *Rhodomonas salina.* Tillmann et al. (2009) investigated clonal variability of *Alexandrium tamarense* and their production of secondary metabolites in a bioassay with *Rhodomonas salina* using the same target species as Busch (2016). In their study, Tillmann et al. (2009) found a huge variety of EC_{50} between the clones. In comparison with these clones, the *A. catenella* strain used in my experiment and tested by Busch (2016) exhibited an intermediate lytic-activity. Blossom et al. (2012),in contrast, found an effect concentration (EC_{50}) of 3000 *A. catenella* cells ml^{-1} (clone K-1490, isolated in Saanich Inlet, Canada) for immobilisation of 50% of the target cell *Heterocapsa rotunda.*

In my experiment, biomass changes of single species and overall diversity changes cannot be ascribed to single traits of *Alexandrium,* such as mixotrophic feeding, allelopathy or nutrient storage capacity, as we could not quantify any of these processes in particular. However, I assume that *Alexandrium* had an advantage and a higher competitive strength under lower nutrient conditions through either one or a combination of these traits.

The local increase of relative *Alexandrium* biovolume contributions caused an increased evenness. The local increase of evenness was found for the NU_{const} treatments for both days

analysed after the addition of *Alexandrium*, but for the NU_{grad} treatment only for the last day of the experiment. This indicates that *Alexandrium* affects phytoplankton evenness under constant nutrient conditions more than under heterogeneous nutrient conditions, where nutrient concentrations had a stronger impact on community composition than the introduction of *Alexandrium*. The most important local difference between the flasks was the nutrient condition. According to these conditions, communities developed differently within the first days, and evenness clearly varied between the positions along the nutrient gradient, with a higher evenness under lower nutrient concentrations. These differences in evenness might also have influenced the invasion success of *Alexandrium* in addition to the nutrient conditions, as community structure might alter competitiveness.

Even though evenness had not been considered much in HAB research, I would like to emphasize, that in this study *Alexandrium* influence was stronger in more even communities and that the introduction of *Alexandrium*, in turn, led to an increase in evenness when dispersal was possible. However, it is important to consider, that evenness is only high when all species are equally abundant. Thus, an increasing *Alexandrium* contribution can increase evenness; however if it exceeds initial imbalance and becomes more dominant, it can again decrease the evenness.

Regional dynamics

Overall, I found weaker effects of *Alexandrium* on the regional scale, due to the rapid growth of the diatom *Thalassiosira,* which dominated the entire experiment, especially in high nutrient levels in the NU_{grad} treatment. This great impact of *Thalassiosira* through the large proportion of the high nutrient flasks led to a decrease in the relative contributions of all other species including *Alexandrium*. Relative contributions of *Alexandrium* were, therefore, higher in the NU_{const} treatments compared to the NU_{grad} treatments.

Local dynamics showed that heterogeneous distribution of resources promoted diversity and evenness, as both were higher under low nutrient concentrations. However, this was not reflected in the regional biomass. Regional biomass was strongly influenced by *Thalassiosira* at highest nutrient concentration, which overshadowed the influence of the enhanced evenness at lower nutrient concentrations, resulting in opposite regional results. In contrast,

Matthiessen et al. (2010), who studied effects of dispersal and resource heterogeneity on marine benthic microalgae, found a higher regional richness, diversity and evenness under resource (light) heterogeneity compared to homogenous resources, although overall light intensity was lower at heterogeneous environments. The environmental gradient promoted diversity and evenness through the reduction of dominance (Matthiessen et al., 2010).

On a regional scale, the initiation position of *Alexandrium* did neither affect total community biomass, nor the relative regional biovolume contributions of *Alexandrium*. Total biovolume in low nutrient flasks of the NU_{grad} treatment was much lower compared to high nutrient concentrations. Consequently, more even distributions of species within the low nutrient flasks contributed only very little to the overall biovolume and as a consequence to the overall regional evenness. Hence regional evenness was lower in the NU_{grad} treatments than in the NU_{const} treatments. This is in contrast with my expectation that evenness would increase in landscapes that are more heterogeneous. Schreiber & Killingback (2013) modelled an evolutionary game in patchy landscapes and found that dispersal promoted local coexistence under spatial heterogeneity. The local evenness of the NU_{grad} treatment with dispersal exhibited strong variations along the nutrient gradient, which reflected the more diverse heterogeneous landscape. However, regional evenness highly depended on the immense influence of only *Thalassiosira* and thus resulted in a lower evenness compared to the homogenous NU_{const} treatments.

Conclusion

This study was, to my knowledge, the first approach to study harmful algae ecology in a spatial context in a meta-ecosystem set-up. This setup proved to be a suitable method to study HAB dynamics in complex spatial systems.

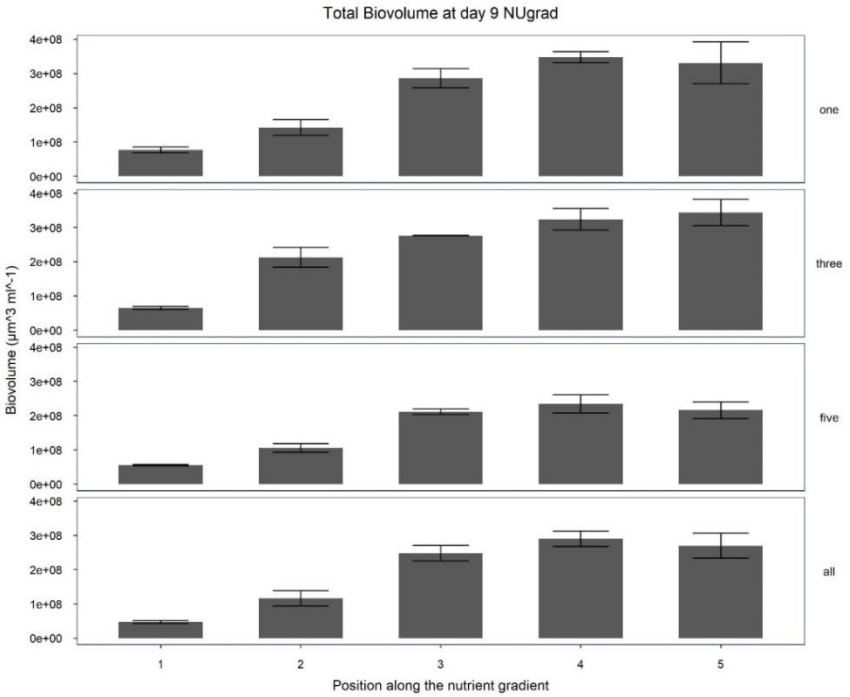
Overall, this study showed very different results on a local and on a regional scale, as on a regional scale, effects of *Alexandrium* were quite weak, whereas local effects showed more distinct patterns of *Alexandrium* presence. The *Alexandrium* dominance in this experiment was patchy and restricted to low nutrient conditions. In natural environments, HABs often occur in a patchy distribution and are therefore highly dependent on local environmental

conditions. These results showed that on the regional scale species could have a weak impact, while they have strong influences on habitats within the local scale.

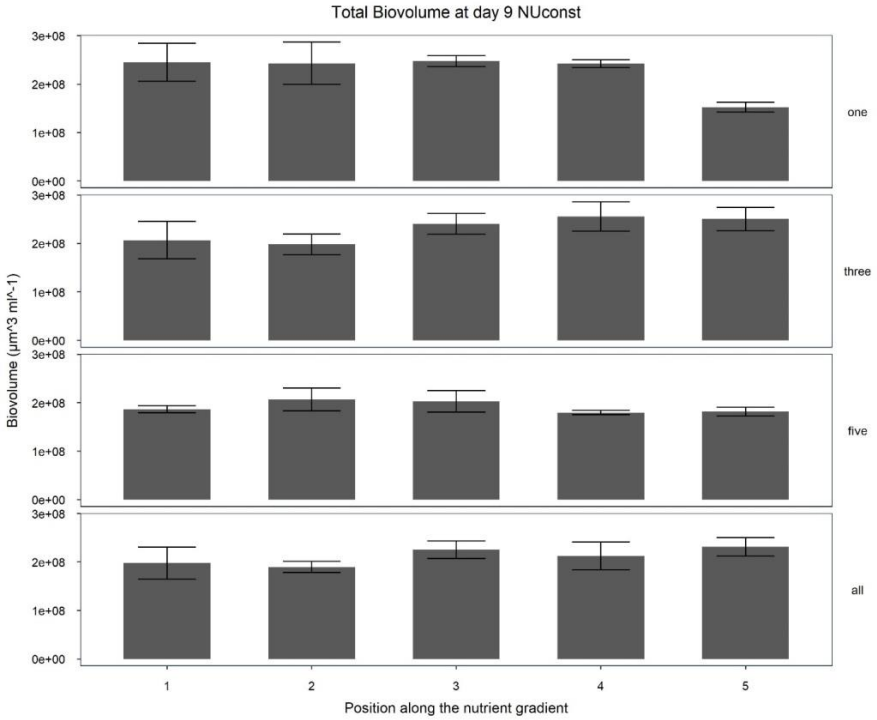
The inoculation position of *Alexandrium* had a huge influence on the dominance over the time course of the experiment. However, I only tested one dispersal time, and it is conceivable, that the influence of the inoculation position is dependent on the overall dispersal rate. Especially, since the lack of dispersal resulted in a much stronger dominance of *Alexandrium*, indicating, that dispersal can weaken bloom formation. It would, therefore, be important to test the responses of *Alexandrium* under different dispersal times in such a system. While the inoculation position was manipulated in this experiments, in natural systems, *Alexandrium* transportation and propagation is highly dependent on ocean currents. Cell transportations via ocean currents are an important mechanism of all HAB propagations, and the species-specific traits, local abiotic and biotic conditions, such as nutrient conditions and community composition seem to be crucial for the establishment of all blooms. As part of this, including more trophic levels into such a meta-ecosystem would be important, to understand harmful algal blooms in their biotic surrounding. Studying harmful algae in their ecological and spatial context can help to understand bloom dynamics and patterns, which in return can help to improve forecasts and management plans.

APPENDIX

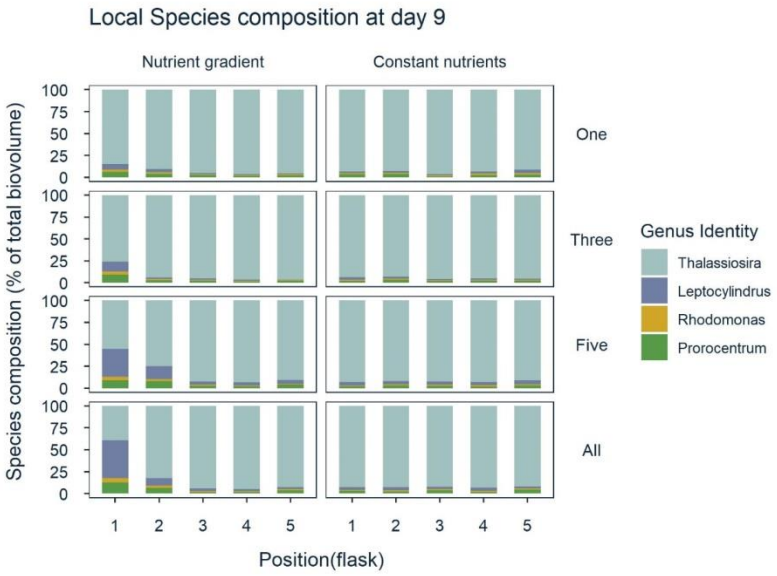
Local



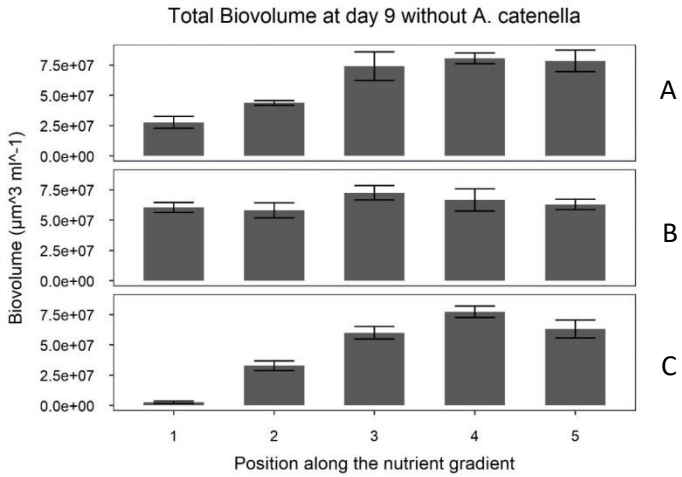
App Figure 1 *Mean local biovolume ± SEat day 9 for the different initiation positions of A. catenella (one, three, five, all) along the nutrient gradient; A. catenella was added at day9, after this sampling*



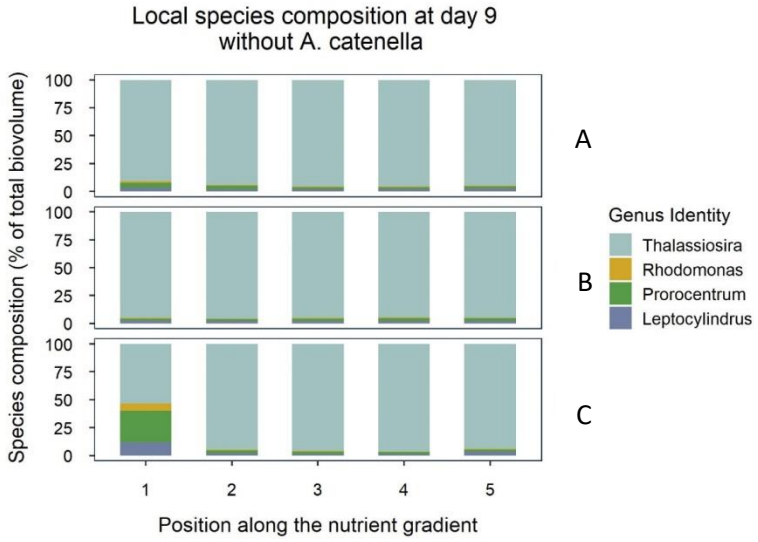
App Figure 2 *Mean local biovolume ± SEat at day 9 for the different initiation positions of A. catenella (one, three, five, all) in constant nutrient meta-ecosystems; A. catenella was added at day9, after this sampling*



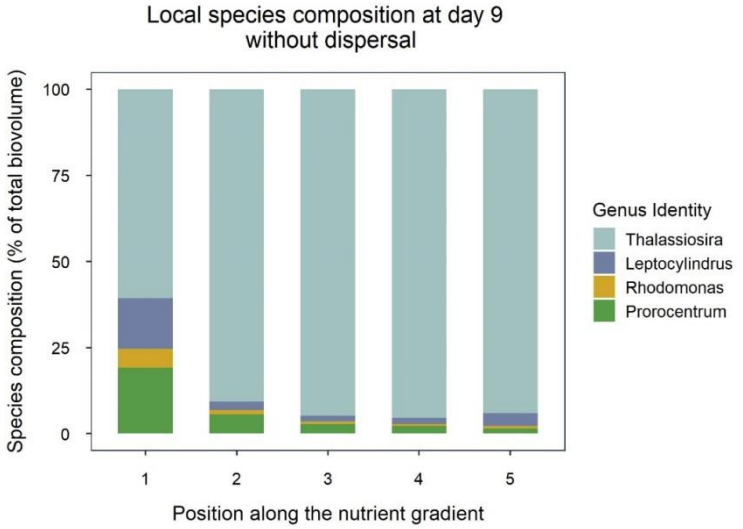
App Figure 3 *Local species composition (as percentage of the total biovolume) at day 9, the day of the A. catenella initiation (one, three, five, all) for NU_{grad} and NU_{const}*



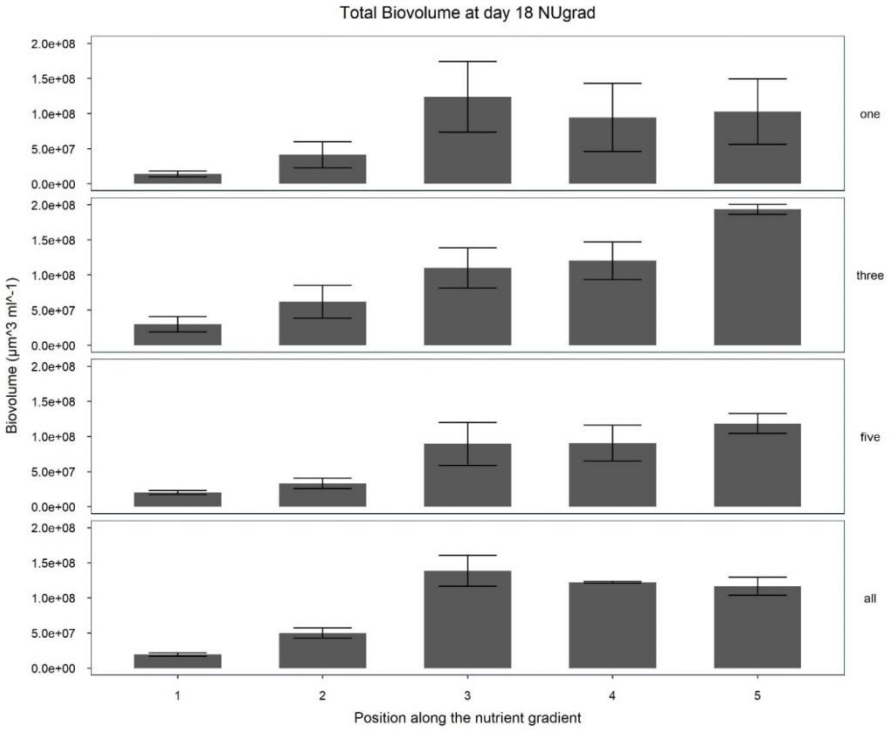
App Figure 4 *Mean local biovolume ± SE at day 9, without the addition of A. catenella; A: NU_{grad} with dispersal, B: NU_{const} with dispersal, C: NU_{grad} without dispersal*



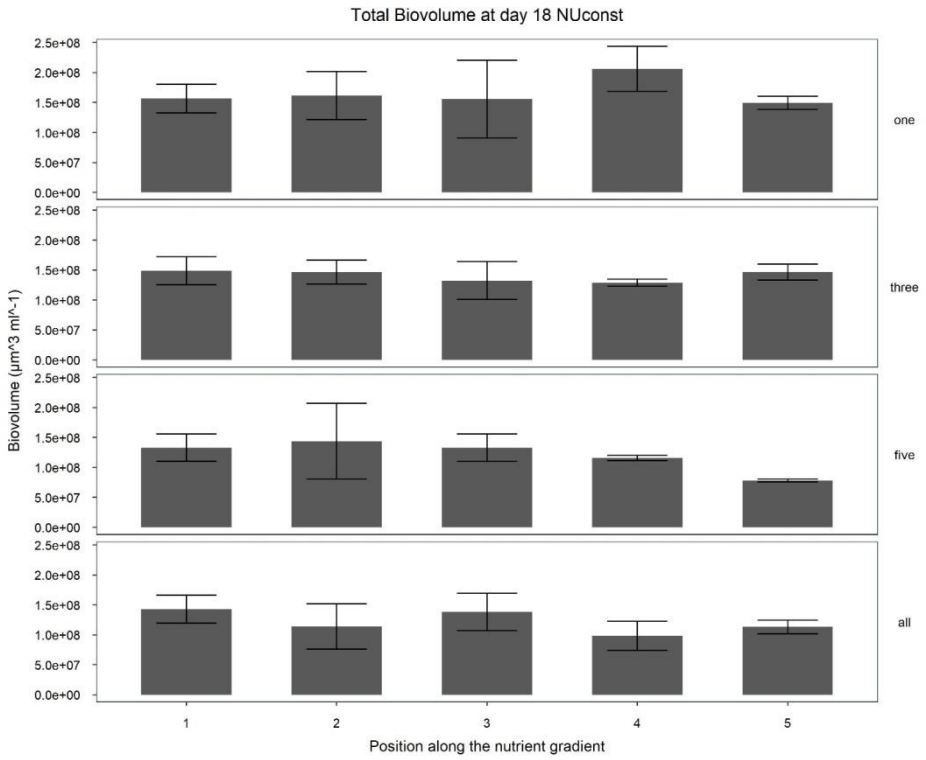
App Figure 5 *Local species composition (as percentage of the total biovolume) at day 9, without the addition of A. catenella; A: NU_{grad} with dispersal, B: NU_{const} with dispersal, C: NU_{grad} without dispersal*



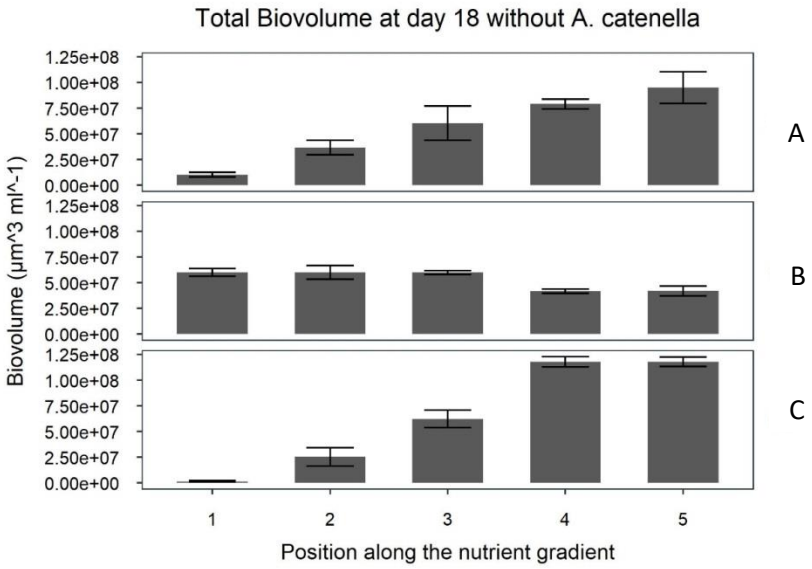
App Figure 6 *Local species composition (as percentage of the total biovolume) at day 9, without dispersal. A. catenella was introduces into all positions at this day (day9)*



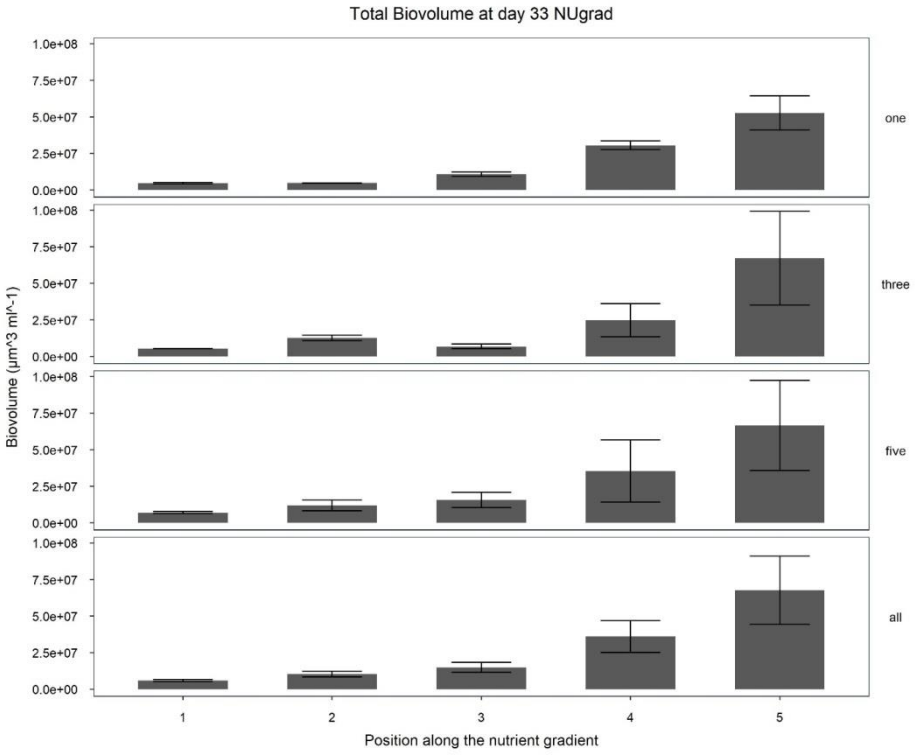
App Figure 7 Mean local biovolume ± SE *at day 18 for the different initiation positions of A. catenella (one, three, five, all) along the nutrient gradient; A. catenella was added at day9, after this sampling*



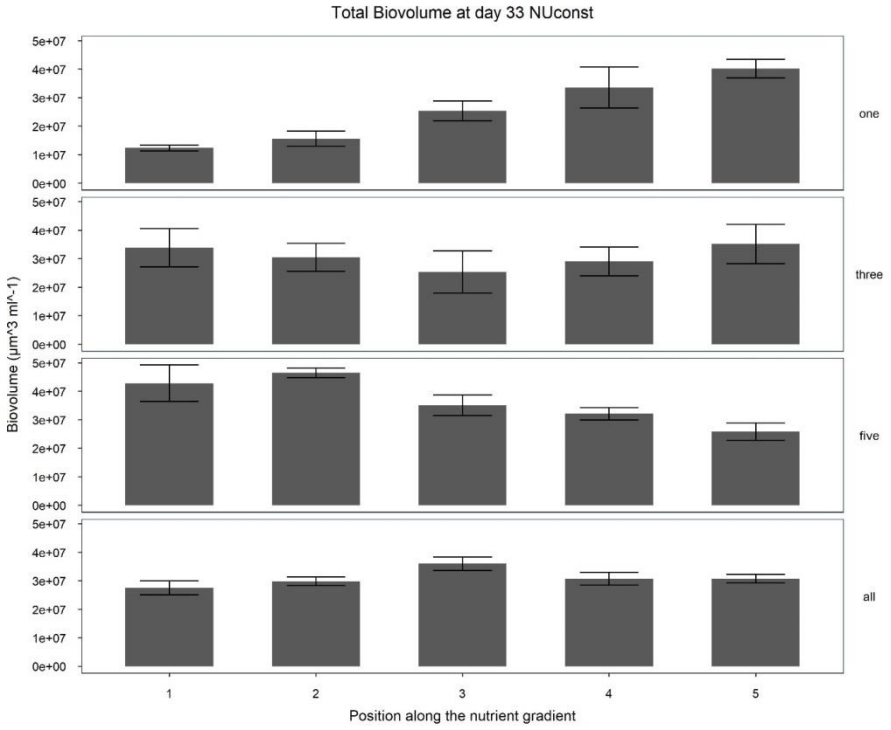
App Figure 8 *Mean local biovolume ± SE at day 18 for the different initiation positions of A. catenella (one, three, five, all) in constant nutrient meta-ecosystems; A. catenella was added at day9, after this sampling*



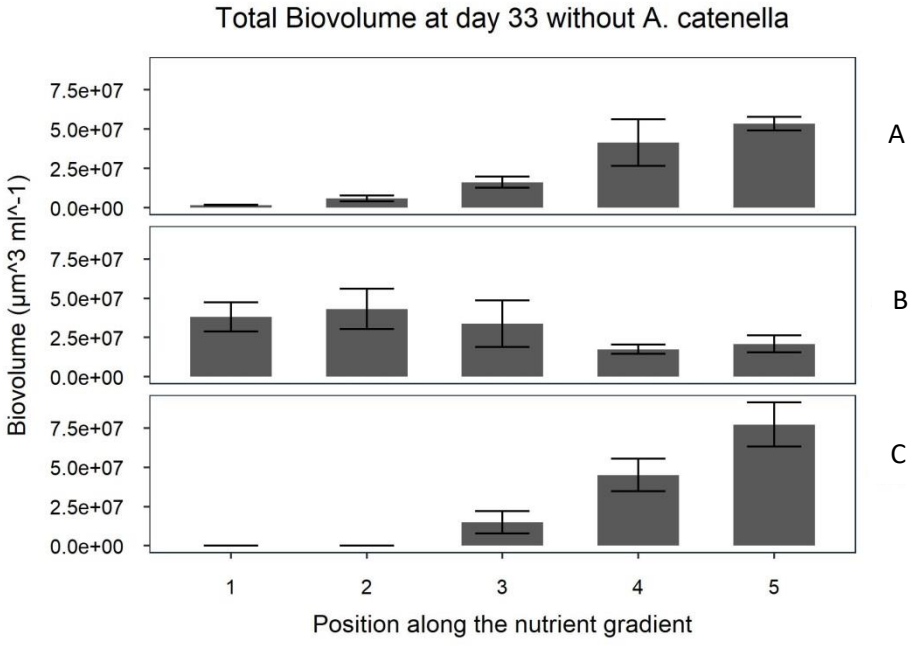
App Figure 9 *Mean local biovolume ± SE at day 18, without the addition of A. catenella; A: NU_{grad} with dispersal, B: NU_{const} with dispersal, C: NU_{grad} without dispersal*



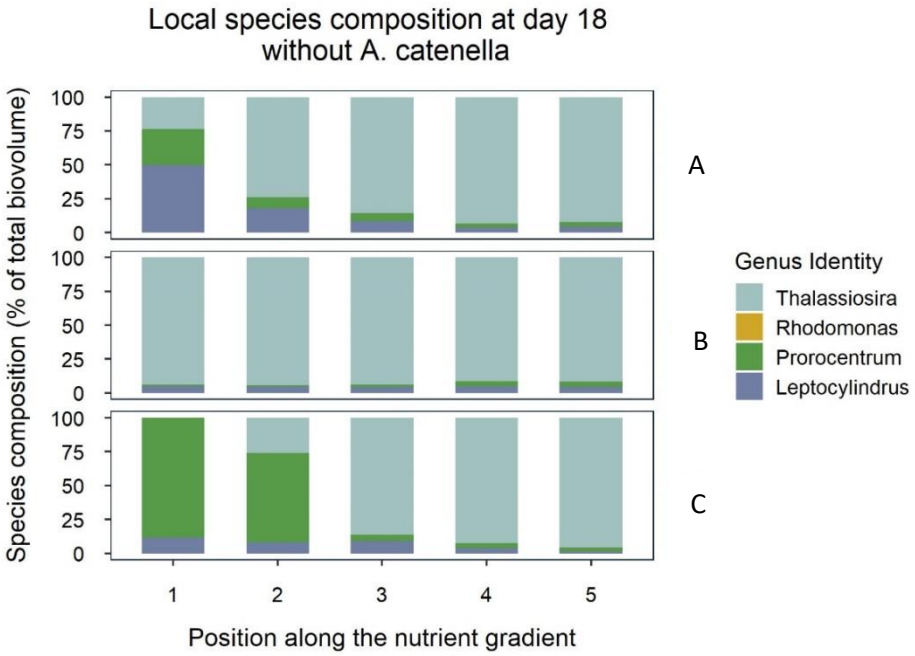
App Figure 10 *Mean local biovolume ± SE at day 33 for the different initiation positions of A. catenella (one, three, five, all) along the nutrient gradient; A. catenella was added at day9, after this sampling*



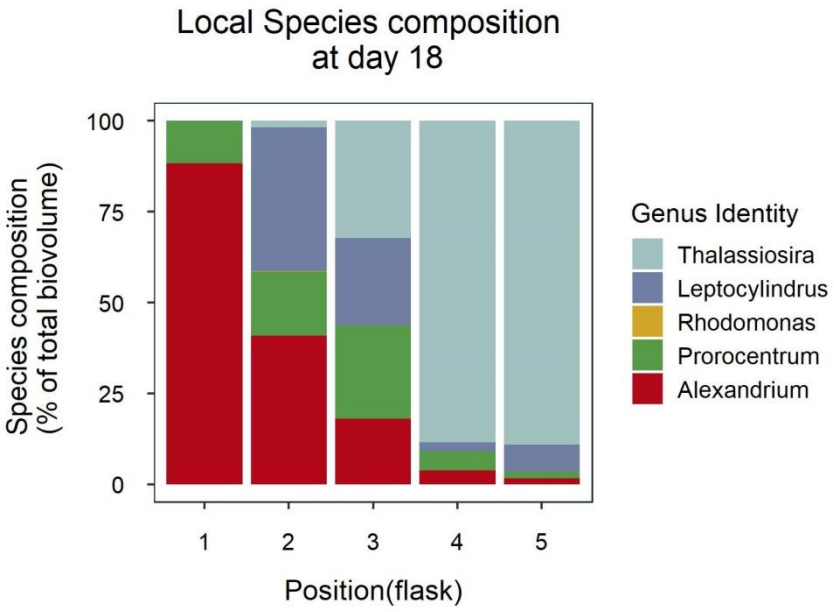
App Figure 11 *Mean local biovolume ± SE at day 33 for the different initiation positions of A. catenella (one, three, five, all) in constant nutrient meta-ecosystems; A. catenella was added at day9, after this sampling*



App Figure 12 *Local total biovolume at day 33, without the addition of A. catenella; A: NU_{grad} with dispersal, B: NU_{const} with dispersal, C: NU_{grad} without dispersal*



App Figure 13 *Local species composition (as percentage of the total biovolume) at day 33, without the addition of A. catenella; A: NU_{grad} with dispersal, B: NU_{const} with dispersal, C: NU_{grad} without dispersal*



App Figure 14 *Local species composition (as percentage of the total biovolume) at day 33, without dispersal. A. catenella was introduces into all positions at day 9*

App Table 1A &B A: ANOVA results of day 9, 18 and 33 for the analyses of local total biovolume, evenness and percentage of A. catenella without dispersal, but with the addition of A. catenella at day 9; B: Post Hoc results show which position they significantly differ from;

A ANOVA results

Response	Day	Transformation (lambda)	Coefficient	dfN	F value	P value
Biovolume	9	0.79	Position	4	43.51	**<0.001**
			Residuals	10		
	18	0.29	Position	4	522.3	**<0.001**
			Residuals	10		
	33	0.11	Position	4	35.69	**<0.001**
			Residuals	10		
Evenness	9	-1.42	Position	4	29.36	**<0.001**
			Residuals	10		
	18	-0.33	Position	4	75.99	**<0.001**
			Residuals	10		
	33	-0.08	Position	4	7.417	**0.0048**
			Residuals	10		
% A. catenella	9	-0.79	Position	4	43.51	**<0.001**
			Residuals	10		
	18	-0.12	Position	4	27.49	**<0.001**
			Residuals	10		
	33	0.14	Position	4	53.8	**<0.001**
			Residuals	10		

B

Response	Day	Position	1	2	3	4	5
Total Biovolume	9	Total Biovolume	2,3,4,5	1,3,4,5	1,2	1,2	1,2
	18		2,3,4,5	1,3,4,5	1,2,4,5	1,2,3	1,2,3
	33		3,4,5	4,5	1,4,5	1,2,3	1,2,3
Evenness	9	Evenness	3,4,5	3,4,5	1,2	1,2,	1,2
	18		3,4,5	3,4,5	1,2,4,5	1,2,3	1,2,3
	33		x	4,5	4,5	2,3	2,3
Percentage of *A. catenella*	9	Percentage of *A. catenella*	2,3,4,5	1,3,4,5	1,2	1,2	1,2,
	18		2,3,4,5	1,3,4,5	1,2	1,2	1,2
	33		3,4,5	4,5	1,4,5	1,2,3	1,2,3

App Table 2A &B A: ANOVA results of day 9, 18 and 33 for the analyses of local total biovolume and evenness without dispersal and A. catenella; B: Post Hoc results show which position they significantly differ from;

A

Response	Day	Transformation (lambda)	Coefficient	dfN	F value	P value
Biovolume	9	0.84	Position	4	43.75	**<0.001**
			Residuals	10		
	18	0.50	Position	4	72.43	**<0.001**
			Residuals	10		
	33	0.11	Position	4	89.63	**<0.001**
			Residuals	10		
Evenness	9	-0.94	Position	4	7.98	**0.00371**
			Residuals	10		
	18	-0.70	Position	4	63.52	**<0.001**
			Residuals	10		
	33	0.36	Position	4	2.846	0.0819
			Residuals	10		

B

Response	Day	Position	1	2	3	4	5
Total Biovolume	9	Total Biovolume	2,3,4,5	1,3,4,5	1,2	1,2	1,2
	18		2,3,4,5	1,3,4,5	1,2,4,5	1,2,3	1,2,3
	33		3,4,5	3,4,5	1,2,4,5	1,2,3	12,3
Evenness	9	Evenness	2,3,4,5	1	1	1	1
	18		2,3,4,5	1,3,4,5	1,2,4	1,2,3,5	1,2,4
	33		x	x	x	x	x

Regional

App Table 3 *Results of the Kruskal-Wallis test from day 9, 18 and 33 for the analyses of regional total biovolume and evenness without the addition of A. catenella at day 9, but with dispersal*

Response	Day	Transformation (lambda)	Coefficient	dfN	P value
Biovolume	9	1.35	Gradient	1	0.8195
	18	0.79	Gradient	1	0.7557
	33	0.407	Gradient	1	0.1524
Evenness	9	-1.81	Gradient	1	0.7244
	18	-0.22	Gradient	1	0.4429
	33	0.02	Gradient	1	**<0.005**

Chapter 2

The effects of community succession and competition on the spatial propagation of L. polyedra along a nutrient gradient

Abstract

The dinoflagellate *Lingulodinium polyedra* is known to form massive blooms, which are commonly known as red-tides. As these blooms can lead to oxygen depletion, *L. polyedra* is considered a harmful algae species. It is necessary to understand their bloom dynamics to improve modelling approaches and future predictions of harmful algae blooms in highly productive regions, such as upwelling systems. However, specific bloom onset mechanisms and bloom dynamics seem to be complex and still not fully understood.

It was the aim of this study to investigate bloom development and propagation of *L. polyedra* in a temporal and spatial context of a meta-ecosystem experiment. In this set-up of interconnected flasks, the influence of dispersal, nutrient availability and community succession on the bloom dynamics of *L. polyedra* was investigated along a nutrient gradient. To investigate dynamics of this high biomass bloomer, *L. polyedra* was either added into highest or lowest nutrient concentrations and either together with the other phytoplankton species at the beginning of the experiment or after an initial establishment phase of the community for nine days.

Overall, diatoms were extremely dominant in all positions along the nutrient gradient, whereas dinoflagellates only contributed minor fractions to the community biovolume. Although *L. polyedra* did not bloom, it performed significantly better under lower nutrient concentrations. Adittionally the inoculation position along the nutrient gradient improved its performance, as it promoted their ability to compete with other community members when inoculated under lowest nutrient conditions.

The results of this study indicate, that nutrient input and phytoplankton community composition, including their successional state and competition between species, are important determinants for bloom dynamics of *L. polyedra* harmful dinoflagellates.

Introduction

Harmful algae blooms have been of economic and ecological interest for centuries. As some harmful blooms discolour the water brownish-red or red, harmful algal blooms (HABs) have been called "red tides" for a long time. *Lingulodinium polyedra* (F. Stein) J. D. Dodge 1989 (former *Gonyaulax polyedra* or *Lingulodinium polyedrum*) is a dinoflagellate species which often produces massive blooms and thus causes red tide events. It is widely distributed and occurs in Europe, North and South America, as well as in Oceania (Lassus et al., 2016). *L. polyedra* is categorized as a harmful algal bloom (HAB) species, as it forms high-density blooms, which can reach cell abundances of more than 2×10^7 cells L^{-1}, and their subsequent demise can lead to oxygen depletion due to bacterial degradation (Allen, 1946; Bruno et al., 1990; Hayward et al., 1995; Holmes et al., 1967; Kahru and Mitchell, 1998; Marasovic, 1989). This lack of oxygen can kill invertebrates and fish (Horner et al., 1997). Thus *L. polyedra* can have a severe ecological and economic impact on the entire ecosystem. In addition, *L. polyedra* produces yessotoxin (YTX), a phycotoxin, which had lethal effects on mice when injected intraperitoneal (Armstrong and Kudela, 2006; Aune et al., 2002; Tubaro et al., 2003). YTX was shown to have cardiotoxic effects and to target the immune system, the lysosomes and the thymus (Alfonso *et al.*, 2016). However, the precise mechanism of YTX is still unknown and to date YTX has neither been shown to have toxic effects on humans nor marine mammals in the Southern California Bight (Paz *et al.*, 2004, 2008; Caron *et al.*, 2010; Alfonso *et al.*, 2016). The Southern Californian Bight, where *L. polyedra* blooms occur regularly, is a coastal upwelling region. It has a highly dynamic nutrient regime, with occasional strong nutrient

input through upwelling events, where cold and nutrient-rich deep water is transported to the surface (Checkley and Barth, 2009; Ryan et al., 2009). This region is, therefore, a hot-spot for phytoplankton growth, including the growth of different HAB species, which can lead to health issues and economic losses (Hoagland et al., 2002; Horner et al., 1997). As inorganic nutrient input generates strong competition for dissolved nutrients, phytoplankton biomass and community composition are highly influenced by each upwelling event. To improve modelling approaches and future predictions of HABs in such upwelling regions and potentially even prevent ecological and economic losses, it is crucial to understand the species-specific traits of the target species, e.g. regarding nutrient uptake and competition with other phytoplankton groups to understand their bloom dynamics.

Diatom blooms generally emerge with or shortly after upwelling events in well-mixed waters (Kudela et al., 2005; Margalef, 1978). Dinoflagellates, in contrast, mostly bloom after nutrients have already been depleted. As a consequence, *L. polyedra,* as well as dinoflagellates in general, often bloom during the relaxation period after the upwelling event under stratified water and warm weather conditions (Allen, 1946; Garrison, 1979; Holmes et al., 1967; Horner et al., 1997; Smayda and Trainer, 2010). Thus, the potential of dinoflagellates to form a bloom is highly influenced by the nutrient-driven competitive interactions between dinoflagellates and diatoms, which is shaped by the intensity, duration and ratio between upwelling and relaxation periods (Margalef, 1978; Vidal et al., 2017). *L. polyedra* blooms may also occur after high nutrient freshwater runoff through heavy rainfalls, such as in March 1995, where *L. polyedra* formed a massive bloom in Southern California, which was attributed to the strong freshwater nutrient input in combination with a strong stratification (Hayward et al., 1995).

Overall, diatoms are known to be good competitors for dissolved inorganic nutrients, as they mostly have higher maximum nutrient uptake rates than dinoflagellates, as well as relatively high maximum growth rates, whereas marine dinoflagellates generally exhibited lower maximum growth rates (Litchman et al., 2007). However, dinoflagellates have evolved different strategies to increase their competitive strength under nutrient-poor conditions. One of the reasons why dinoflagellates can thrive in regions with dynamic nutrient conditions might be their ability to store large amounts of organic and inorganic nitrogen forms (Dagenais-Bellefeuille and Morse, 2013; Maguer et al., 2007). Furthermore, many dinoflagellates are mixotrophs (Jeong et al., 2005a, 2005b; Yoo et al., 2009): they obtain energy by the ingestion and subsequent breakdown of organic particles, as well as through

photosynthesis. In addition to increased nutrient uptake, mixotrophy is advantageous as it may decrease the competitive pressure through the consumption of potential competitors. Busch (2016) found mixotrophic feeding of *L. polyedra* especially when dissolved inorganic nutrients were depleted. Hence mixotrophy could give *L. polyedra* a competitive advantage over strict phototrophs (e.g. Stoecker *et al.*, 2006; Burkholder *et al.*, 2008). Thus, both strategies, nutrient storage and mixotrophic feeding, can potentially help *L. polyedra* to thrive in nutrient-limited environments. Some other dinoflagellates are known to produce lytic allelopathic metabolites that can negatively influence growth, reproduction and survival of co-existing organisms (Granéli et al., 2008; Inderjit and Dakshini, 1994; John et al., 2014b; Rice, 1983). However, this strategy has not been found for *L. polyedra* (Busch, 2016).

Upwelling regions are often hot-spots for both diatoms and dinoflagellates, and this strong interaction also shaped bloom dynamics of *A. catenella* in Chapter 1. In addition, a study on the Alboran Sea (Western Mediterranean Sea) showed that dinoflagellate dominance depended on the proportion of diatoms which changed along a nutrient gradient from the coast to offshore, hence emphasising the importance of competing species and community composition for dinoflagellate success (Mercado et al., 2014)

Despite the pronounced influence of nutrients in upwelling regions, other factors, such as hydrodynamic transport and dispersal via ocean currents have been found to determine the propagation of HABs and consequently their bloom dynamics (Bialonski et al., 2016; Franks and Kaefer, 2003). Circulation patterns, for instance, can be highly variable in upwelling systems, depending on, e.g. physical and topographic characteristics of the continental shelf (Kudela et al., 2005; Meunier et al., 2010). Bialonski et al. (2016) studied the influence of transportation via ocean currents, local hydrography and environmental factors on HAB propagation within the Southern California Bight. Transportation was an important factor shaping the expansion and distribution of some taxa, whereas environmental conditions, such as coastal upwelling, had a stronger influence on other taxa (Bialonski et al., 2016). Ryan et al. (2009) demonstrated for Monterey Bay (California) that local properties and connectivity could influence regional dynamics, as dense red-tide dinoflagellate blooms developed in the inner shelf waters of this coast, functioning as “bloom incubators”, and could rapidly spread due to changes in wind and water movement. Their study indicated that while winds and currents influenced bloom propagation, bloom formation was promoted under favourable local environmental conditions. Overall, these studies showed, that spatial scales play an

important role for bloom dynamics, as local and regional conditions can influence blooming and propagation patterns differently. Additionally, when cells are transported into a new habitat, local environmental factors, as well as community composition, determines if the HAB species can establish in this habitat.

Specific bloom onset mechanisms and bloom dynamics of many HAB species in upwelling regions seem to be complex and still not fully understood. Although spatial aspects have been shown to influence bloom dynamics, dispersal and propagation of HABs have mostly been studied in monitoring and modelling studies. Monitoring field studies often cover larger spatial ranges and provide important information on potential factors promoting bloom dynamics, such as nutrient availability, temperature and upwelling patterns (e.g. Glibert *et al.*, 2008; Vidal *et al.*, 2017). Especially analyses of current patterns and other abiotic and biotic patterns can help to understand bloom propagation. However, such monitoring studies can only correlate different environmental factors to bloom dynamics, whereas controllable laboratory studies help to identify causal relationships between population dynamics and particular environmental factors. The disadvantage of laboratory studies, however, which are mainly conducted in closed systems, is the limitation of space. Hence, in order to understand interactive effects of dispersal and local environmental factors on local and regional dynamics of HABs, spatial dynamics need to be considered not only in the field but also in controlled laboratory experiments.

In recent years, the concept of meta-ecosystems has received increased attention, as it includes spatial dynamics in controllable laboratory studies, connecting aspects of both, laboratory and field approaches. Meta-ecosystems are defined as connected ecosystems which are linked by the spatial flow of energy, materials, as well as organisms (Loreau et al., 2003). With these more complex spatial laboratory setups, both local and regional aspects of community dynamics can be considered in meta-ecosystem studies. These systems have successfully been used to study spatial dynamics of protists and phytoplankton in combination with environmental factors such as nutrient fluxes or perturbations (e.g. Harvey et al., 2016; Limberg et al., 2017; Gülzow et al., 2019). While HABs have been shown to be transported along various chemical and physical gradients, up to date, little attention has been paid to assessing spatial HAB dynamics in meta-ecosystems.

In Chapter 1, I have used a meta-ecosystem, similar to Gülzow et al. (2019), of five interconnected flasks, to investigate ecological interactions and spatial dynamics of the toxic and allelopathic HAB dinoflagellate *Alexandrium catenella* along a nutrient gradient. With this meta-ecosystem setup, I was able to study the effect of nutrient concentrations and heterogeneity on both local and regional dynamics of *A. catenella* in competition with potentially co-occurring phytoplankton species from the Southern California Bight. In addition, I investigated if the inoculation position of the HA species would affect its population dynamics and spatial propagation and if the inoculation into a specific position along the environmental gradient particularly promotes its bloom formation. This laboratory meta-ecosystem experiment was the first approach to study HAB dynamics in a spatial context, which included dispersal along a nutrient gradient. *A. catenella* was a better competitor under lower nutrient concentrations and dominated the community when it was inoculated into the lowest nutrient position. Dispersal had a negative effect on the bloom intensity of *A. catenella*, as its dominance was much stronger when dispersal was excluded. The results of Chapter 1 nicely demonstrated the dependence of HAB dynamics on nutrient concentration and dispersal. However, *A. catenella* was inoculated after nine days into the assembled algae communities, which were strongly influenced by different nutrient concentrations, as especially diatoms strongly increased with increasing nutrient availability. Therefore, different nutrient conditions led to different successional stages of the communities along the nutrient gradient. Hence, the initial community composition and also evenness nine days after inoculation differed along the nutrient gradient and could have influenced invasibility and thus *A. catenella* bloom success in addition to nutrients and dispersal.

Such an improved knowledge of spatial dynamics can help to understand bloom dynamics in upwelling regions, where especially nutrients are highly variable. It is, therefore, the aim of this study to use a similar meta-ecosystem as in Chapter 1, to investigate the spatial dynamics of the high biomass bloomer *L. polyedra* along a nutrient gradient. In addition, community dynamics and competition between *L. polyedra* and the other species of the community were a major focus of this study. In this experiment, I, therefore, studied the interplay of nutrients and community succession on *L. polyedra* bloom dynamics. Hence, I investigated if the inoculation position and timing along a nutrient gradient influences *L. polyedra* bloom patterns, as community succession and development depends on the nutrient concentration

and establishment time without *L. polyedra*. *L. polyedra* was either added into highest or lowest nutrient concentrations and either together with the other phytoplankton species at the beginning of the experiment or after an initial establishment phase of the community for nine days, similar to *A. catenella* in Chapter 1.

Specifically, I tested the following hypotheses:

H1. Along the nutrient gradient, community biomass increases with increasing nutrient concentrations, while evenness decreases. Under favourable conditions, i.e. under low nutrient concentrations, *L. polyedra* becomes more dominant and thus increases overall community biomass, due to its ability to form high-density blooms

H2. *L. polyedra* increases in dominance, when inoculated into the lowest nutrient position, as these are the most favourable conditions for its competitive success, due to its potential to store nutrients and feed mixotrophically.

H3. *L. polyedra* achieves a higher competitive success when inoculated at the later time point, as nutrients are expected to quickly decrease and better promote the success of *L. polyedra* at a later time point under lower nutrient concentrations.

H4. For H2 and H3, effects of *L. polyedra* will be stronger on the local scale than on the regional scale, as inhomogeneous local dynamics will be levelled out at a regional scale.

Methods

In this experiment, we investigated both spatial and temporal aspects of the initiation and bloom dynamics of the harmful dinoflagellate *L. polyedra* along a nutrient gradient, i.e. the competitive success of *L. polyedrum* depending on the position and timing of inoculation into an assembled phytoplankton community.

Medium preparations and laboratory culture conditions

In this experiment, the same phytoplankton community as in *Experiment 1* (Chapter 1) was used, except for *A. catenella*, which was exchanged by the red tide dinoflagellate *Lingulodinium polyedrum*. The high biomass bloomer *L. polyedrum* has a mixotrophic lifestyle and can thus potentially ingest other cells. Community species selection was based on natural occurrences in the Southern Californian Bight, as they have all been isolated in this region (David Caron Laboratory, University of Southern California, Los Angeles, USA). I assembled a community consisting of three different taxonomic groups, with the cryptophyte *Rhodomonas abbreviata*, two diatoms, *Thalassiosira sp.* and *Leptocylindrus sp.*, as well as the non-toxic dinoflagellates *Prorocentrum micans*.

Biovolume was used as a proxy for algal biomass. Individual cell volumes were calculated according to the geometrical shapes of the cells (Hillebrand et al. 1999), based on microscopically measuring the dimensions of 30 randomly chosen individuals of each species (Axiophot, Zeiss). Initial biovolume of all species (μm^3 ml^{-1}) was determined of the stock cultures prior to the experiment.

All phytoplankton stock cultures were maintained in f/2 medium (Guillard, 1975; Guillard and Ryther, 1962), which was prepared with autoclaved North Sea water taken from the Jade Bay (Wilhelmshaven, Germany). Our non-axenic stock cultures were kept in culture flasks (TC-Flasks T75, Sarstedt) at 18°C in a constant environment at a light intensity of 80 µmol m^{-2} s^{-1} in a 12:12h light: dark regime.

Table 1 Medium composition: Nitrogen (N), Phosphorous (P) and Silicate (Si) concentrations (µmol L^{-1}) in the five different mediums

Medium	N (µmol L^{-1})	P (µmol L^{-1})	Si (µmol L^{-1})
M1	28.91	1.98	59.95
M2	72.66	4.18	59.95
M3	104.98	5.99	59.95
M4	144.66	8.27	59.95
M5	187.84	10.74	59.95

Prior to our experiment, five culture media, similar to the media in Chapter 1, differing in nitrogen and phosphorus concentrations were prepared using sterilised North Sea water (M1-M5; Tab. 1). According to the f/2 medium (Guillard, 1975; Guillard and Ryther, 1962), trace

metals and vitamins were added. Media nutrient concentrations increased evenly and were adjusted to the Redfield-ratio (Redfield, 1934). Silicate (Si) was not adjusted to the gradient, as natural Si concentrations were already high, with 59.95 µmol $L^{-}1$, which is more than four times higher than the lowest Si concentration in Chapter 1 (Tab.1 Chapter 1) Table (Chapter 1&2). M1 represented the lowest nutrient concentration, whereas M5 represented the highest. In order to reduce the additional nutrient input into the experiment by adding phytoplankton from stock cultures, all stock cultures were pre-incubated on nutrient reduced medium (M3) for seven days prior to the experiment.

Meta-ecosystem setup and experimental design

In order to investigate propagation, trophic interactions and the effect of inoculation timing of *L. polyedra* along a nutrient gradient, I conducted a meta-ecosystem experiment, using a similar meta-ecosystem set up as in Chapter 1. The meta-ecosystem was set-up similar to Gülzow et al. (2019) and consisted of five interconnected 50ml Erlenmeyer flasks (DURAN). Flasks were connected via 6cm long silicon tubes (5 mm Ø, TYGON), which were attached to customized glassy tube conjunctions on two sides. Tubes were kept close with locking clips (Bevara, IKEA), and only opened for 2min of dispersal daily (see Chapter 1).

Each flask of the meta-ecosystems was filled with 55ml of the respective medium, resulting in an increasing nutrient gradient from flask 1 to flask 5 (M1-M5; Tab. 1). A total algal biovolume of $4x10^6$ μm^3 ml^{-1} was added per flask. The algae inoculum consisted of the four species, *Rhodomonas abbreviata, Prorocentrum micans, Thalassiosira* sp. *and Leptocylindrus* sp.. All species were set up with an even biovolume of $1x10^6$ μm^3 ml^{-1}, equal to an evenness of 1, to compensate for major variances in cell size.

In order to test the influence of inoculation timing and position of *L. polyedra* on its bloom dynamics along the nutrient gradient, *L. polyedra* was either added at the beginning of the experiment together with the other four species or after an establishment phase of the community for nine days. At both time points, *L. polyedra* was either added into position 1 or 5, which reflected the lowest and the highest nutrient concentrations along the gradient, to investigate the influence of nutrient supply on competitive interactions with this dinoflagellate. For the treatments of the early dinoflagellate inoculation (position 1 ($Start_{one}$)

or 5 ($Start_{five}$)), *L. polyedra* was intended to be added to the communities with an equal biovolume as the other species to keep the evenness of 1. However, due to a miscalculation, *L. polyedra* was added with a higher biovolume of $3x10^6$ μm^3 ml^{-1}, resulting in a *L. polyedra* dominated community and an initial evenness of 0.9 in the meta-ecosystems. For the later *L. polyedra* addition nine days after incubation, *L. polyedra* was added with a biovolume of $1x10^7$ μm^3 ml^{-1} into the highest ($Late_{five}$) or the lowest ($Late_{one}$) nutrient concentration, similar to the initial inoculation biovolume of *A. catenella* in Chapter 1. This biovolume was one order of magnitude higher than the initial inoculation biomass of each community species (and more than three times higher than the initial *L. polyedra* inoculation), to compensate for initial growth and to give *L. polyedra* the opportunity to compete with the other species. In addition, a control without *L. polyedra* was established to evaluate the potential effects of this dinoflagellate on the phytoplankton community regarding competition and/or mixotrophic feeding. All of the five treatments were set up as triplicates, resulting in 15 meta-ecosystems, with a total of 75 flasks.

All meta-ecosystems were randomly placed and fixed on a shaking table (Laboshake, Gerhardt) with a rotation speed of 80rpm, which was tested prior to the experiment (see Chapter 1) to ensure dispersal of all species, but at the same time to sustain the nutrient gradient over the five flasks of the meta-ecosystem. The experiment ran for 24 days in a temperature controlled climate chamber at 18°C (± 2°C) and an average light intensity of 100 $\mu mol\ m^{-2}\ s^{-1}$ with a constant 12:12 day : night rhythm. Light intensity and water temperature in the flasks were logged continuously using data loggers (Onset HOBO Pendant® data logger).

This experiment was sampled semi-continuously. Every third day, 15% of the total volume of each flask was removed (8.25ml) and subsequently replaced with the respective medium (M1-M5, Tab. 1) to maintain the nutrient gradient. Only at day nine, the replaced volume of the medium of the $Late_{one}$ and $Late_{five}$ treatments varied due to the additional inoculation of *L. polyedra*. Here, the added medium was reduced by the volume, which was added through the *L. polyedra* addition (4.51ml medium, 3.74ml *L. polyedra* culture).

At every sampling, chlorophyll *a* was measured with a fluorometer (TURNER DESIGNS, AquaFluor™) in 3.25ml of the removed volume. For microscopic cell counting, the same samples were fixed with 10% Lugols iodine in amber glass bottles. The remaining 5ml of the samples were filtered through cellulose acetate syringe filters (Chromafil CA 20/25, Macherey-

Nagel) and stored at -20°C, for subsequent analysis of dissolved nutrients (nitrogen, phosphorus and silicate). Samples for particulate nutrients (carbon, nitrogen, phosphorus) were only taken on day 0, 9 and 24 of the experiment. In order to have a sufficiently high volume to take samples for particulate nutrients of the phytoplankton communities in different nutrient treatments just before the *L. polyedra* addition at day nine, I set up three additional sets of meta-ecosystems (three replicates) at the beginning of the experiment, which were terminated at day nine (without *L. polyedra* only). For particulate nutrients, a volume of 20ml was filtered through a pre-combusted and acid washed GF/F filter (Ø25 mm, Whatman). For each sample, two filters were used (one for carbon and nitrogen analysis, one for phosphate analysis). Filters were stored at -20°C until further analysis.

Nutrient analysis

Filters for particulate nutrients analyses (carbon, nitrogen, phosphorus) were dried in a compartment drier at 40°C. Filters for particulate P were additionally combusted for 2h at 550°C. Particulate CN analyses were conducted using a CHN analyser (Thermo Scientific; FlashEA, 1112 Series). Particulate P was photometrically measured as orthophosphate following the method of Wetzel & Likens (2003).

Dissolved nutrient samples (nitrogen, phosphorus, silicate) were measured using a photometric autoanalyzer (SKALAR; SAN++ System).

Phytoplankton analysis

Algal biovolume and community composition were quantified using an inverted Leica DM IL LED microscope. Due to the different nutrient conditions, cell density varied vastly. Therefore, subsamples of 0.5ml up to 3ml were counted in Utermöhl sedimentation chambers at 100x magnification. A minimum of 10 randomly chosen grids, as well as a minimum of 400 cells, were counted.

Statistical analyses

All graphs and statistical procedures were conducted with R version 3.4.3 (R Core Team, 2017), using the packages vegan, ggplot2, lme4, plyr, emmeans, lmerTest and gridExtrar.

Data were analysed both on the local (every single patch) and the regional scale (each meta-ecosystem) over the entire duration of the experiment.

For local analyses, a linear mixed model was conducted for each response variable: total biovolume, chlorophyll *a*, community evenness, *L. polyedra* total biovolume as well as relative contributions of *L. polyedra*. The effects of the inoculation treatment, which combines timing, position, as well as the control ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$, Control), and the position along the nutrient gradient was tested for each response variable. The position along the nutrient gradient equaled the stepwise increase of the nutrient concentration. As each meta-ecosystem was considered as five units, it was used as a random factor in all models, as flasks were not independent from each other due to their connection. In addition, time was used as a random factor.

Regional analyses were conducted similarly to the local models, also using the same response variables. However, the mean of all five flasks was used instead of the values of each flask. Therefore, only inoculation treatment ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$, Control) was tested, whereas the position along the nutrient gradient/the nutrient concentration was ignored because each meta-ecosystem was only considered as one unit. Each meta-ecosystem and time was used as random factors.

L. polyedra absolute and relative biovolume was only analysed for day 15 until the end of the experiment, as cells were added at day nine and the comparison of the treatments would thus be highly manipulated by the lack of variation on day nine due to equally abundant numbers in the 'Late' addition treatments. However, to account for the temporal offset of the inoculation, I additionally compared two specific dates, using again linear mixed models for all previously mentioned response variables on the local scale. Therefore, nine days and 15 days after *L. polyedra* inoculation were analysed, which were represented by day nine and 18 in the 'Early' treatments and day 18 and 24 in the 'Late' treatment. Models did not include time as a random factor, as they were only conducted for one specific date. In these models, just the four treatments were compared (without Control). Additionally, regional responses were

tested nine and 15 days after *L. polyedra* inoculation using a one-way ANOVA for each response and the Tukey post-hoc test, to compare treatment differences.

In all linear mixed models, both, local and regional, residuals distribution was checked, and data were transformed if residuals were distributed heterogeneously (log and square root transformations; Table 2,3). Significances were quantified using an analysis of variances (ANOVA function in the lmerTest package). If treatments showed significant effects, the emmeans function was used as a post-hoc test to conduct a pairwise comparison of the treatments.

Local particulate nutrient ratios (C:N, C:P and N:P) were analysed with a linear mixed model, with treatment and position as explaining variables as well as meta-ecosystem as a random factor. Time was not included as a random factor, as data were only sampled from all flasks on the last day of the experiment. Effects of the inoculation treatment on the regional particulate nutrient ratios were analysed using a one-way ANOVA for each ratio (C:N, C:P, N:P) and the Tukey post-hoc test, to compare treatment differences

Results

Chlorophyll a and community biovolume

Biomass measured as chlorophyll *a* significantly increased with increasing nutrient concentration, independent of the inoculation position and timing of the *L. polyedra* introduction ($p<0.001$, Tab. 2, 3a&b, Fig. 1). Over time, chlorophyll *a* strongly increased until day 6 (up to 369µg Chl *a* L^{-1} in the highest nutrient position), after which it constantly decreased to levels of 12 - 55µg Chl *a* L^{-1} at the lowest, and 22 - 148µg Chl *a* L^{-1} at highest nutrient concentrations (between day 15-24; Fig.1).

The comparison of chlorophyll *a* between the different inoculation treatments and the control over time as well as between the treatments after equal incubation time with *L. polyedra* (day nine and 15 of the 'early' treatment and day 18 and 24 of the 'late' treatment), showed no effect of treatments alone on the chlorophyll *a* (Tab. 2, 3a&b). However, the comparison nine days after *L. polyedra* inoculation (day nine of the 'early' treatment and day 18 of the 'late' treatments) showed significant differences between the interaction of the inoculation treatments and the positions along the nutrient gradient ($p<0.01$, Tab. 3a), with a much

stronger chlorophyll *a* increase with increasing nutrient concentration in the $Start_{one}$ and $Start_{five}$ treatments. As the $Late_{one}$ and $Late_{five}$ treatments represented day 18 of the experiment, chlorophyll *a* was already much lower and their chlorophyll *a* increase was much weaker with increasing position, i.e. nutrient concentration. Fifteen days after the inoculation of L. polyedra, this interaction chlorophyll *a* had decreased in all treatments and thus did not show any significant interactions.

*Table 2 Results from linear mixed models of the local community testing the effect of different treatments ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$, Control) and the position along the nutrient gradient, as well as their interacion for different responses (A-E). Models were either calculated over the entire course of the experiment (for chlorophyll a, total biovolume and evenness) or from day 15 until the end of the experiment (for absolute and relative L. polyedra biovolume), as the late inoculation of L. polyedra on day 9 highly influences variance. Absolute and relative L. polyedra biovolume were square root transformed. Degree of freedom, F-values and p-values are shown. Significant effects are highlighted bold. [*1,2] refer to corresponding post-hoc pairwise comparison results in the appendix: S1&S2.*

		Factor	df	F	p
A	Chlorophyll *a*	Treatment	4	0,673	0,611
		Position	1	333,524	***<0,001***
		Treatment : Position	4	1,382	0,239
B	Total biovolume	Treatment	4	0,330	0,858
		Position	1	328,778	***<0,001***
		Treatment : Position	4	0,787	0,533
C	Evenness	Treatment	4	0,646	0,630
		Position	1	177,859	***<0,001***
		Treatment : Position	4	0,985	0,415
D	(sqrt transformed) (Absolute) *L. polyedra* biovolume	Treatment	3	21,451	***<0,001*** [*1]
		Position	1	0,121	0,729
		Treatment : Position	3	31,492	***<0,001***
E	(sqrt transformed) Mean relative *L. polyedra* biovolume	Treatment	3	18,301	***<0,001*** [*2]
		Position	1	28,922	***<0,001***
		Treatment : Position	3	29,250	***<0,001***

Table 3 a&b Results from linear mixed models of the local community testing the effect of different treatments ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$) and the position along the nutrient gradient, as well as their interacion for different responses (A-E) nine days (day nine of the 'early' treatment, day 18 of the 'late' treatment) (a) and 15 days (day 15 of the 'early' treatment, day 24 of the 'late' treatment) (b) after *L. polyedra* incubation. Degree of freedom, F-values and p-values are shown. Significant effects are highlighted bold. Absolute and relative *L. polyedra* biovolume were square root transformed. *1,2,3,4,5 refer to corresponding post-hoc pairwise comparison results in the appendix: S3- S7.

a

		Factor	df	F	p
A	Chlorophyll *a*	Treatment	3	2.174	0.107
		Position	1	377.587	***<0.001***
		Interaction	3	59.674	***<0.01***
B	Total biovolume	Treatment	3	0.682	0.564
		Position	1	102.463	***<0.001***
		Interaction	3	4.032	***<0.01***
C	Evenness	Treatment	3	4.371	***<0.01****1
		Position	1	39.956	***<0.001***
		Interaction	3	3.910	***<0.05***
D	(sqrt transformed) (Absolute) *L. polyedra* biovolume	Treatment	3	11.337	***<0.001*** *2
		Position	1	0.022	0.882
		Interaction	3	14.745	**<0.001**
E	(sqrt transformed) Relative *L. polyedra* biovolume	Treatment	3	23.439	***<0.001*** *3
		Position	1	20.014	***<0.001***
		Interaction	3	24.029	***<0.001***

b

		Factor	df	F	p
A	Chlorophyll a	Treatment	3	0.436	0.728
		Position	1	14.550	***<0.001***
		Interaction	3	0.839	0.479
B	Total biovolume	Treatment	3	1.004	0.396
		Position	1	194.237	***<0.001***
		Interaction	3	6.725	***<0.001***
C	Evenness	Treatment	3	1.973	0.133
		Position	1	103.157	***<0.001***
		Interaction	3	2.493	*0.072*
D	(sqrt transformed) (Absolute) *L. polyedra* biovolume	Treatment	3	5.406	***<0.01*** [*4]
		Position	1	1.283	0.264
		Interaction	3	6.661	**<0.001**
E	(sqrt transformed) Relative *L. polyedra* biovolume	Treatment	3	7.376	***<0.001*** [*5]
		Position	1	4.743	***<0.05***
		Interaction	3	7.824	***<0.001***

Regional chlorophyll *a* levels followed a similar temporal trend compared to local dynamics, with an initial increase, followed by a decrease, which was independent of inoculation position and timing in the model over the full-time period (Fig. 2; Tab. 4). Different inoculation timing treatments, however, differed after nine days' incubation time with *L. polyedra* (i.e. day nine and 15 of the 'early' treatment and day 18 and 24 of the 'late' treatment, Tab. 5a, Appendix S7), showing significantly lower chlorophyll *a* in both late inoculation treatments, compared to the early inoculation treatments. Similar to the local interactive effects, it needs to be considered that successional states of the overall communities differed between those treatments, as they represented the community at day nine and day 18.

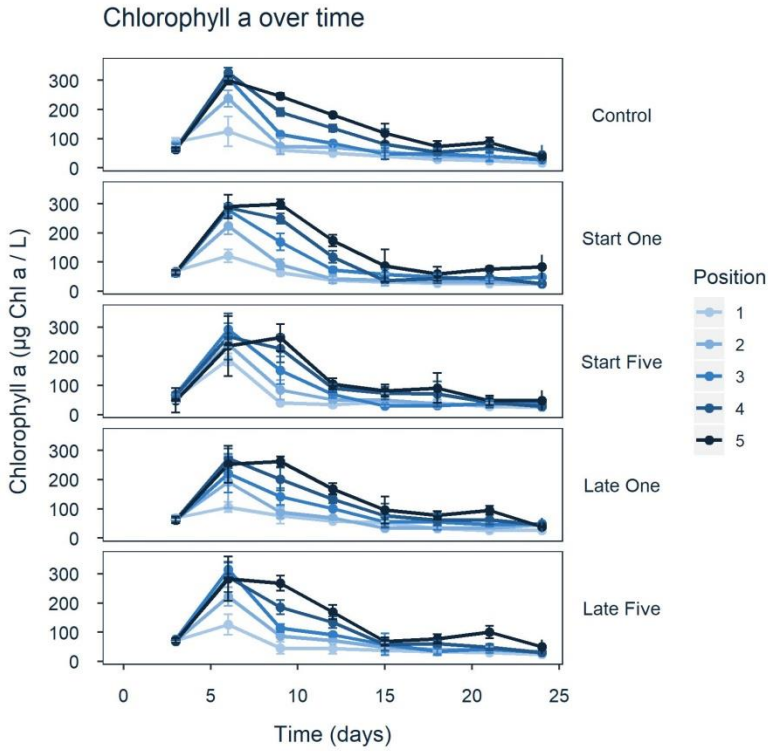


Figure 1 Mean local chlorophyll a ± SD (µg L^{-1}) over time. Plots are split up into L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$). Colors indicate the increasing nutrient concentration in the respective position from light (position 1) to dark blue (position 5).

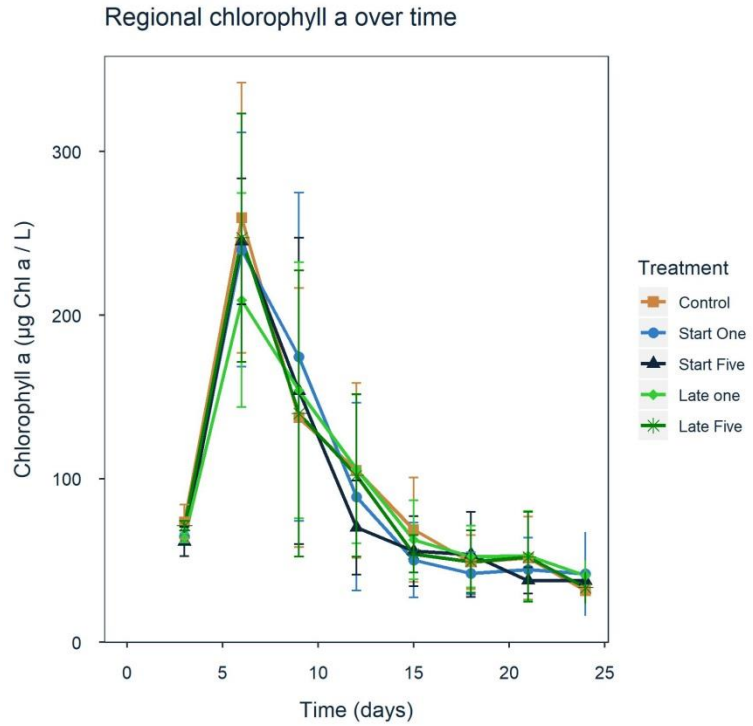


Figure 2 Mean regional chlorophyll a ± SD (µg L^{-1}) over time. Regional means were calculated from the mean of all five flasks of one meta-ecosystem. L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$) are represented by different colors.

Table 4 Results from linear mixed models of the regional community, testing the effect of different treatments ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$, Control) for different responses (A-E). Regional responses were calculated by the mean of all five flasks of one meta-ecosystem. Chlorophyll a and relative L. polyedra biovolume were square root transformed. Degree of freedom, F-values and p-values are shown.

		Factor	df	F	p
A	(sqrt) Chlorophyll *a*	Treatment	4	1,188	0,320
B	Total biovolume	Treatment	4	1,495	0,275
C	Evenness	Treatment	4	1,218	0,312
D	(Absolute) *L. polyedra* biovolume	Treatment	3	1,477	0,293
E	(sqrt transformed) Relative *L. polyedra* biovolume	Treatment	3	0,888	0,488

Local and regional biovolume calculated from microscopic cell counts showed comparable biovolume developments (Fig. 3 & 4). Also here, the effect of increasing biovolume with increasing nutrients was significant on the local scale over the entire course of the experiment, as well as in the models comparing treatments of different inoculation timing nine and 15 days after *L. polyedra* inoculation ($p<0.001$, Tab. 2, 3). These results are in accordance with H1, stating that community biomass increases with increasing nutrient concentrations. On the local scale, no differences of the total biovolume between the control and the *L. polyedra* inoculation treatments were observed. However, I found a significant interaction between the treatments and the nutrient gradient nine and 15 days after *L. polyedra* inoculation ($p<0.001$, Tab. 3). Similar to the interactions observed for chlorophyll *a*, this interaction can be ascribed to the different successional states of the overall communities, as they represented the community at day nine and day 18.

Over the entire course of the experiment, total regional biovolume did not show significant differences between the inoculation treatments, including the control (Fig. 4, Tab. 4). However, the comparison of the treatments nine and 15 days after *L. polyedra* inoculation

reflected again the successional state of the communities, as they represent the community after different durations, with a significantly lower total regional biovolume in both late inoculation treatments, compared to the early inoculation treatments (Tab. 4, 5, Appendix S8).

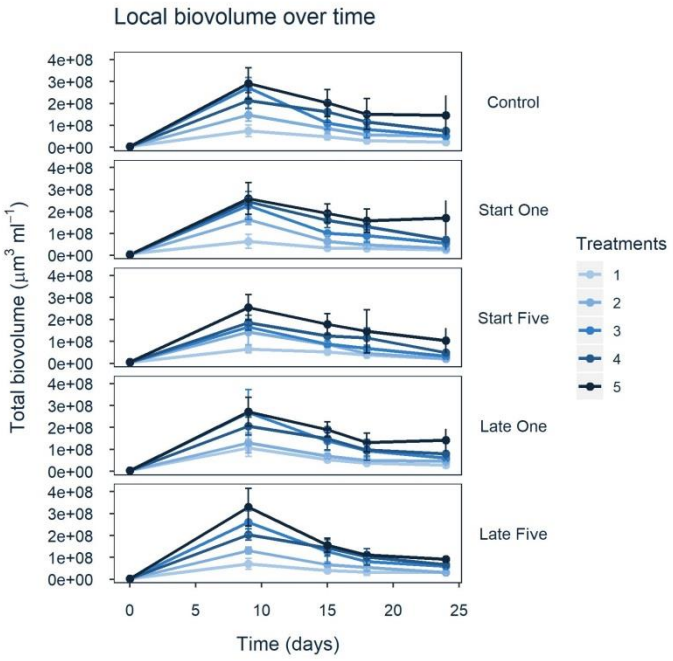


Figure 3 Mean local biovolume ± SD (µm³ ml⁻¹) of the entire community over time. Plots are split up into L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$). Colors indicate the increasing nutrient concentration in the respective position from light (position 1) to dark blue (position 5).

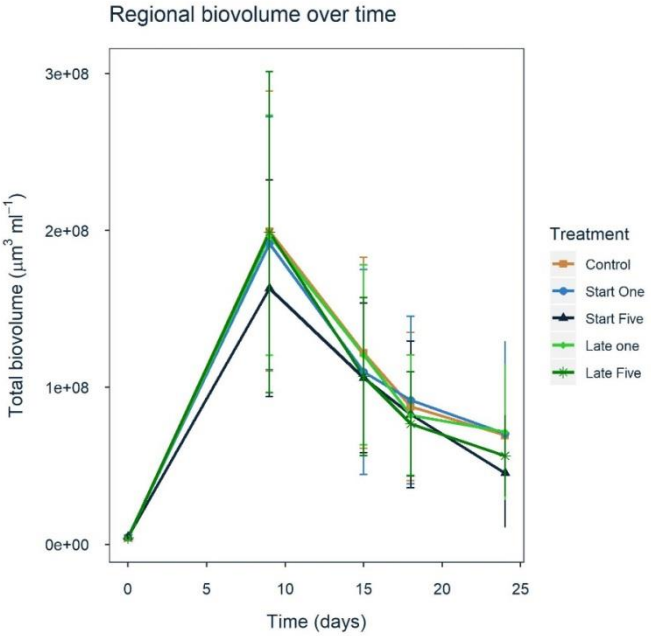
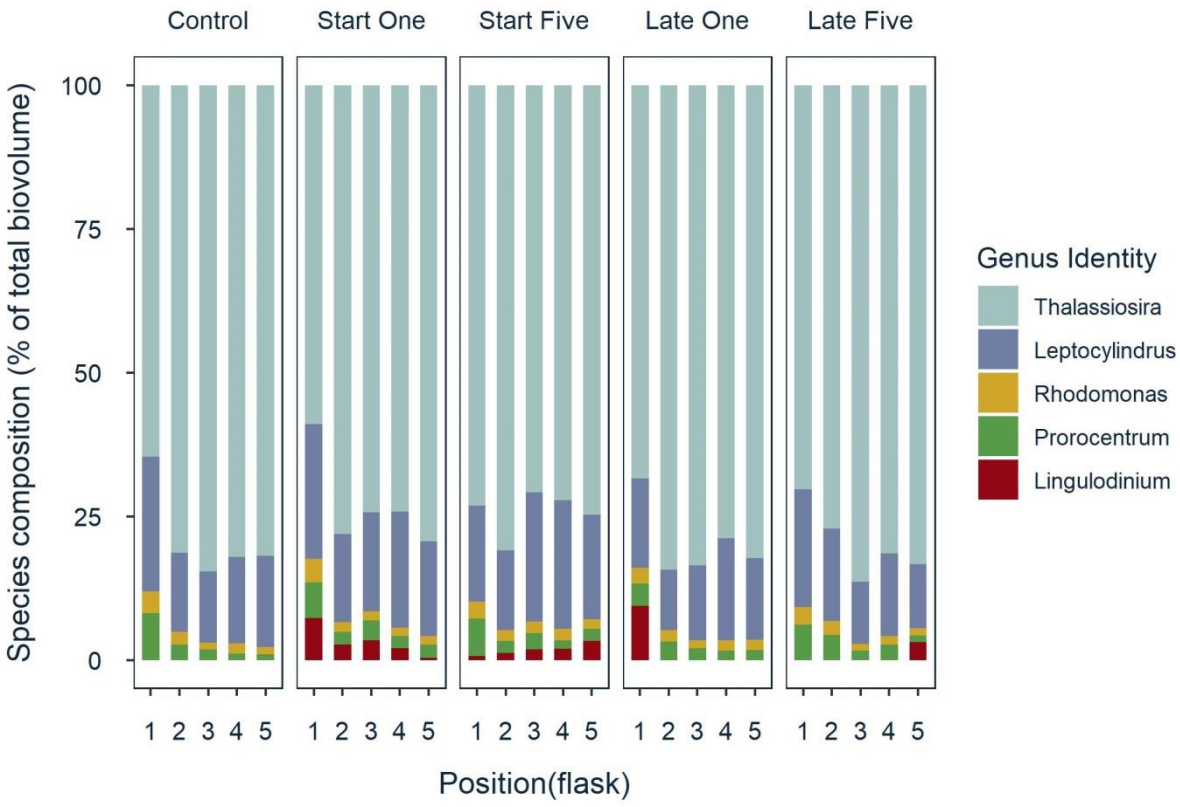
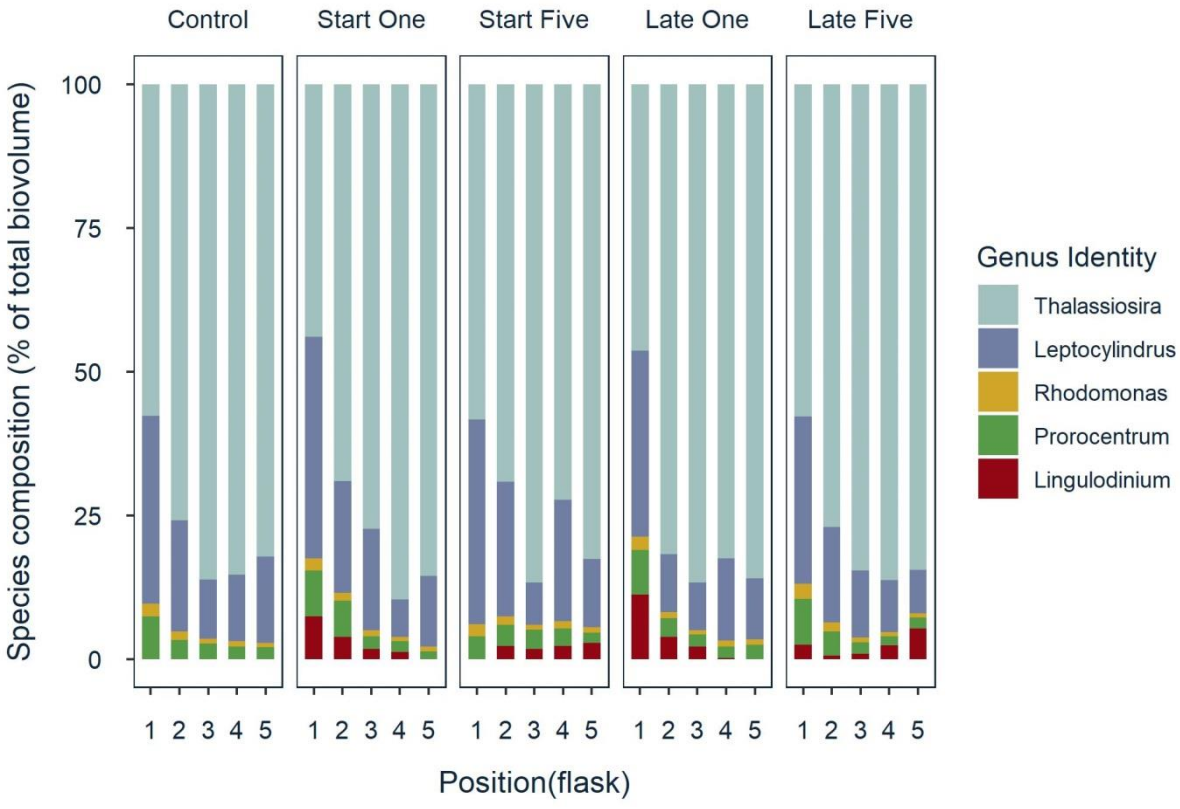


Figure 4 Mean regional biovolume ± SD (µm³ ml⁻¹) of the entire community over time. Regional means were calculated from the mean of all five flasks of one meta-ecosystem. *L. polyedra* inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$) are represented by different colors.

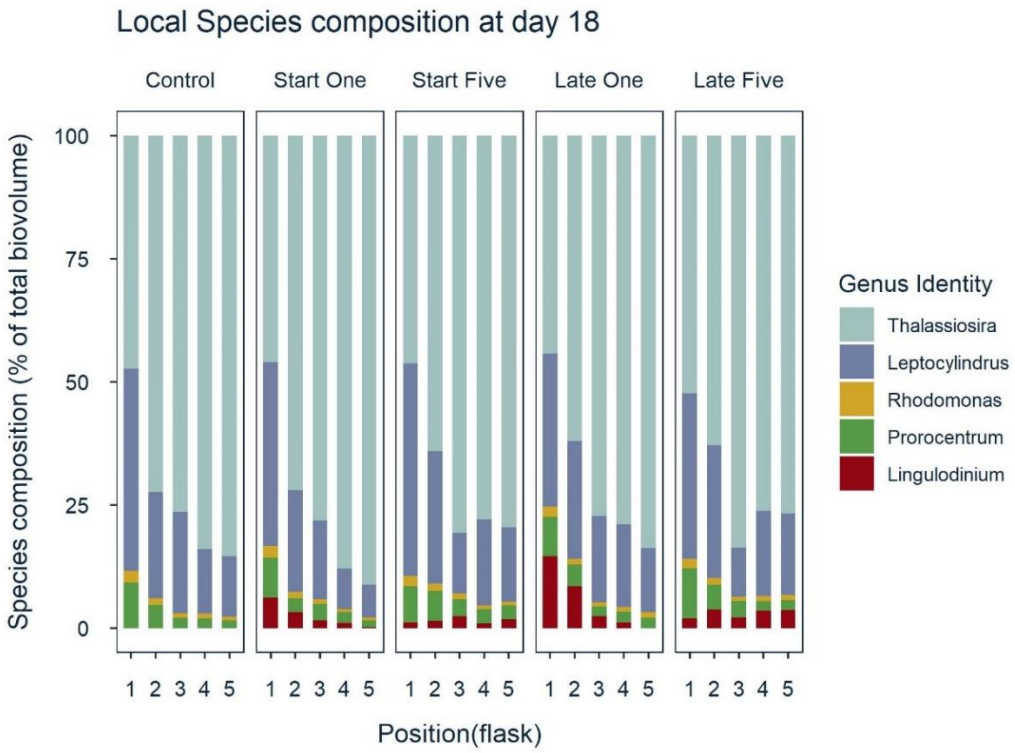
A


Local Species composition at day 9
Control
Start One
Start Five
Late One
Late Five
Species composition (% of total biovolume)
100
75
50
25
0
1 2 3 4 5
Position(flask)
Genus Identity
Thalassiosira
Leptocylindrus
Rhodomonas
Prorocentrum
Lingulodinium

B


Local Species composition at day 15
Control
Start One
Start Five
Late One
Late Five
Species composition (% of total biovolume)
100
75
50
25
0
1 2 3 4 5
Position(flask)
Genus Identity
Thalassiosira
Leptocylindrus
Rhodomonas
Prorocentrum
Lingulodinium

C



D

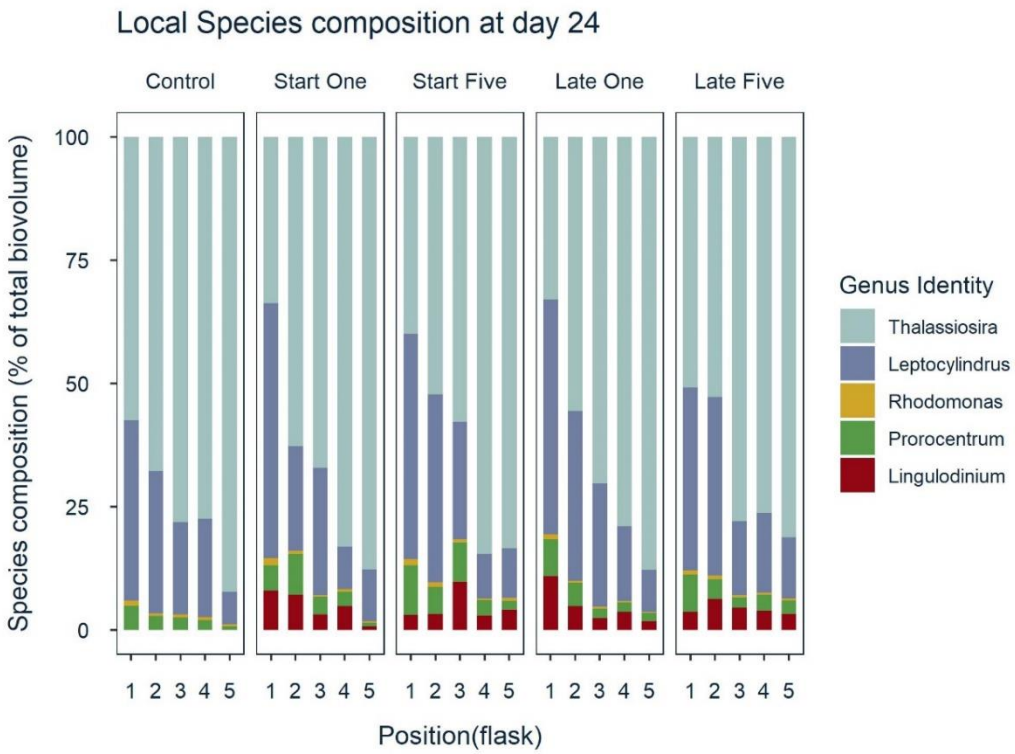


Figure 5 Relative phytoplankton composition (% of the total phytoplankton biovolume) shown as stacked bar charts for A) day 9, B) day 15, C) day 18, D) day 24. Plots are split up into L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$).

Community composition and evenness

The communities were initially set up with equal biovolume and therefore an evenness of 1. When *L. polyedra* was inoculated from the beginning on, it had a higher relative biovolume than the other species, representing an initial biovolume of 44% of the total community, resulting in an evenness of 0.9 in the respective flasks. However, this initial dominance decreased drastically and was replaced mostly by diatoms, where *Thalassiosira sp.* was more abundant than *Leptocylindrus* in the beginning (day nine, Fig. 5A), while the latter had a stronger impact at the end of the experiment (day 24, Fig. 5D). Overall, the effect of *Thalassiosira sp.* was stronger at higher nutrient concentrations, whereas *Leptocylindrus sp*., as well as the dinoflagellates, contributed higher fractions to the community at lower nutrient concentrations (Fig. 5). The relative contribution of *Leptocylindrus sp*. as well as of both dinoflagellates also increased over time. These differences were also reflected in the evenness, which, despite the overall initial decrease, differed among nutrient concentrations with a significantly higher evenness at lower nutrient concentrations and vice versa in all treatments, including the control without *L. polyedra* addition ($p<0,001$; Tab. 2, 3, Fig. 6). I can, therefore, accept the second part of H1, that community evenness decreases with increasing nutrient supply. Treatment effects of the inoculation position or timing of *L. polyedra* on the evenness were only found nine days after equal incubation time with *L. polyedra* (day nine of the 'early' treatment and day 18 of the 'late' treatment), where the model indicated significant differences between the evenness of the inoculation treatments (Tab. 3a). However, significant differences between treatments could not be confirmed with the post-hoc analyses (Tab. 3a, Appendix S3).

On the regional scale, evenness decreased drastically in all treatments, including the control, but remained relatively stable (around 0.5) from day six onwards (Fig. 7). There was no observable difference of the evenness, neither between the *L. polyedra* inoculation treatments, nor between the control and the treatments (Fig. 7, Tab. 4, 5).

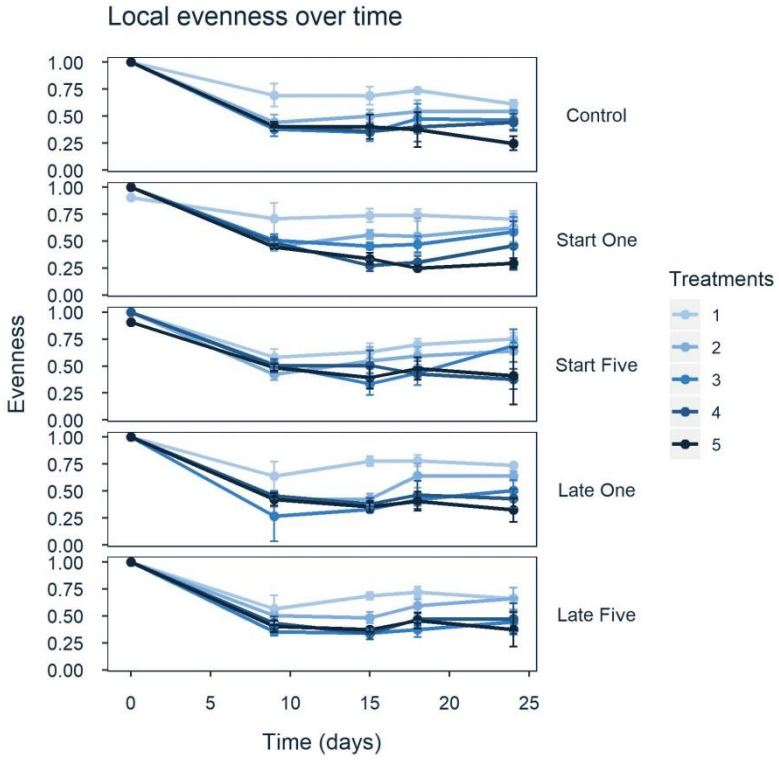


Figure 6 Mean local evenness ± SD over time. An evenness of 1 represents equal portions (biovolume) of all species. Plots are split up into L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$). Colors indicate the increasing nutrient concentration in the respective position from light (position 1) to dark blue (position 5).

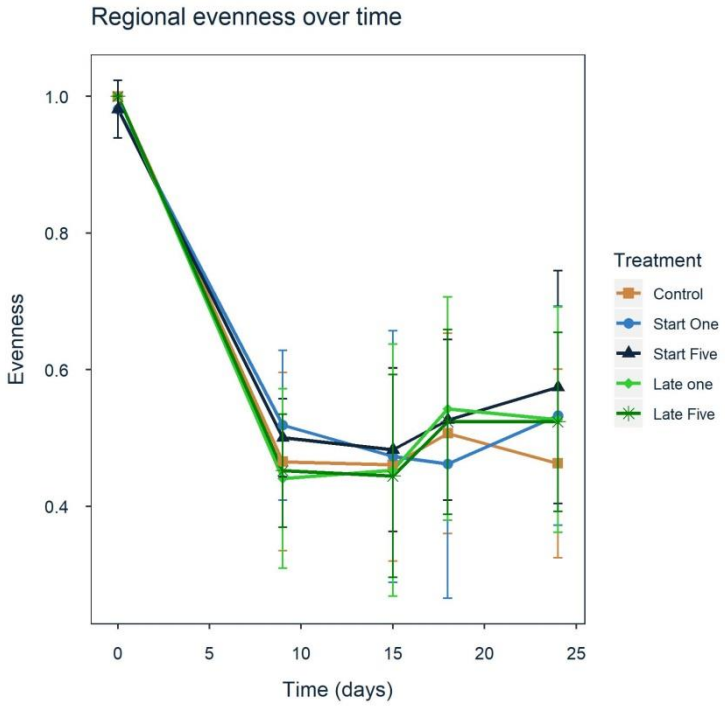


Figure 7 Mean regional evenness ± SD over time. An evenness of 1 represents equal portions (biovolume) of all species. Regional means were calculated from the mean of all five flasks of one meta-ecosystem. L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$) are represented by different colors.

L. polyedra dynamics

L. polyedra was not able to form a bloom, and it was overall the inferior competitor, as its absolute and relative biovolume contributions were overall low. However, relative *L. polyedra* contributions were promoted when inoculated at lower nutrient concentrations, supporting hypothesis H2. While *L. polyedra* relative contributions were overall higher at lower nutrient concentrations, especially when inoculated into this position, inoculation timing played only a minor role for *L. polyedra* dynamics. As a late inoculation promoted neither absolute nor relative *L. polyedra* biovolume, I can reject hypothesis H3. Differences of the *L. polyedra* population dynamics were overall low between the different inoculation treatments, both on the local and the regional scale. Thus, I can neither reject, nor support H4, stating that effects of *L. polyedra* will be stronger on the local scale than on the regional scale, as inhomogeneous local dynamics will be levelled out regionally.

It is worth mentioning that this experiment was sampled semi-continuously; part of the biomass was removed every third day and replaced by fresh medium. Thus, maintaining the same biovolume over a longer period of time, which was observed for *L. polyedra* for almost all treatments until the end of the experiment, represents a steady state, where the input of fresh nutrients resulted in growth, which replaced the removed biomass.

Local effects of L. polyedra

When inoculated at the beginning of the experiment together with all other species, *L. polyedra* absolute biovolume increased during the first days ($Start_{one}$ and $Start_{five}$, Fig.8). This increase was observable despite the strong impact of dilution, as *L. polyedra* quickly dispersed into all connected flasks. From day nine until day 15 or 18, depending on the position, *L. polyedra* absolute biovolume decreased and remained relatively low until the end of the experiment. When *L. polyedra* was introduced at day nine, its absolute biovolume strongly decreased in the inoculated flasks and *L. polyedra*, for the most part, distributed evenly into the other flasks (Fig. 8). At day 24, *L. polyedra* absolute biovolume slightly increased in position four and five of the $Late_{one}$ treatment, representing high nutrient concentrations of the gradient (Fig.8).

Absolute *L. polyedra* biovolume was not significantly influenced by the nutrient gradient (Tab. 2). However, the ANOVA results of the linear mixed model from day 15 until the end of the

experiment, as well as the models which compared the treatments after similar incubation time with *L. polyedra* (day nine and 15 of the 'early' treatment, day 18 and 24 of the 'late' treatment), showed significant differences of the *L. polyedra* biovolume. Differences were found between inoculation treatments as well as between the interactions of the treatments with the position along the nutrient gradient ($p<0.001$, Tab. 2, 3). While the post-hoc tests could not confirm the differences between treatments (Appendix S1, S4, S6), the interaction can be seen, as *L. polyedra* absolute biovolume generally remained higher closer to the initial inoculation position (Fig.8, Appendix S14&15).

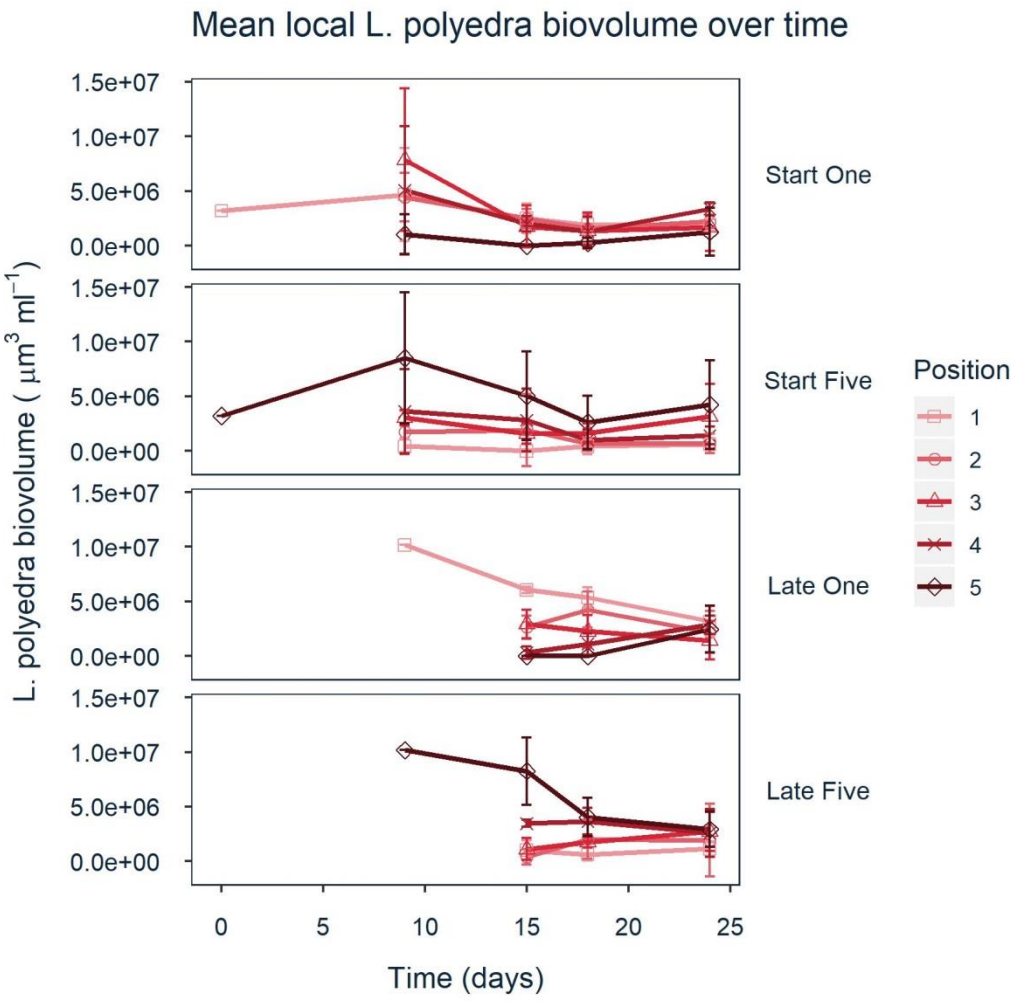


Figure 8 Mean local L. polyedra biovolume ± SD (μm^3 ml^{-1}) over time. Plots are split up into L. polyedra inoculation treatments ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$). Colors indicate the increasing nutrient concentration in the respective position from light (position 1) to dark red (position 5).

Table 5 a&b *ANOVA results for the regional community, testing the effect of different treatments ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$) on different response variables (A-E) nine days (day nine of the 'early' treatment, day 18 of the 'late' treatment) (a) and 15 days (day 15 of the 'early' treatment, day 24 of the 'late' treatment) (b) after L. polyedra incubation. Regional responses were calculated by the mean of all five flasks of one meta-ecosystem. Degree of freedom, Sum of squares, Mean squares, F-values and p-values are shown. Significant effects are highlighted bold. Absolute and relative L. polyedra biovolume were square root transformed. ^{*1,2,3,4} refer to corresponding post-hoc test results (Tukey's HSD) in the appendix: S8-S11.*

a 9 days after *L. polyedra* inoculation

		Factor	df	Sum Sq	Mean Sq	F	p
A	(sqrt transformed) Chlorophyll *a*	Treatment	3	39118	13039	56.31	***<0.001*** ^{*1}
		Residuals	8	1852	232		
B	Total biovolume	Treatment	3	$3.009*e^{16}$	$1.003*e^{16}$	35.98	***<0.001*** ^{*2}
		Residuals	8	$2.230*e^{15}$	$2.787*e^{14}$		
C	Evenness	Treatment	3	0.003	0.001	0.522	0.679
		Residuals	8	0.014	0.002		
D	(Absolute) *L. polyedra* biovolume	Treatment	3	0.653	0.218	1.37	0.32
		Residuals	8	1.272	0.159		
E	Relative *L. polyedra* biovolume	Treatment	3	20.89	6.963	5.361	***<0.05*** ^{*3}
		Residuals	8	10.39	1.299		

b 15 days after *L. polyedra* inoculation

		Factor	df	Sum Sq	Mean Sq	F	p
A	(sqrt transformed) Chlorophyll *a*	Treatment	3	890.2	296.74	4.059	0.0501
		Residuals	8	584.9	73.11		
B	Total biovolume	Treatment	3	$6.161*e^{15}$	$2.054*e^{15}$	10.02	***<0.01*** *4
		Residuals	8	$1.639*e^{15}$	$2.049*e^{14}$		
C	Evenness	Treatment	3	0.007	0.002	0.597	0.635
		Residuals	8	0.031	0.004		
D	*L. polyedra* biovolume	Treatment	3	0.188	0.063	0.192	0.899
		Residuals	8	2.598	0.325		
E	% *L. polyedra* biovolume	Treatment	3	1.677	0.5591	1.489	0.29
		Residuals	8	3.004	0.3755		

Relative *L. polyedra* biovolume was inoculated with a contribution of more than 40% ($Early_{one}$, $Early_{five}$) in the beginning, and therefore with dominance over all other community species. This dominance decreased drastically after which relative *L. polyedra* biovolume, with only a few exceptions, remained stable below 10% until the end of the experiment. When inoculated after nine days ($Late_{one}$, $Late_{five}$), relative biovolume remained more or less stable throughout the experiment.

L. polyedra biovolume contributions were higher closer to its inoculation position. These results are confirmed by the statistical analyses, which showed significant differences between the interaction of the treatments and the position along the nutrient gradient ($p<0.001$, Tab. 2, 3, 4). However, contributions were higher at lowest nutrient concentration, especially when inoculated into this position ($Start_{one}$, $Late_{one}$), whereas it became more similar along the nutrient gradient, when inoculated into the highest nutrient concentration ($Early_{five}$ and $Late_{five}$ treatment, Fig. 5, 10). This promotion under lowest nutrient concentrations was additionally confirmed by the model results, as they revealed a significantly positive effect of decreasing nutrient concentration on the relative *L. polyedra* biovolume ($p<0.05$. Tab. 2, 4, 5). While the models also showed significant effects of the

treatments alone on the relative *L. polyedra* biovolume ($p<0.001$. Tab. 2, 4, 5), these differences could not be confirmed through the post-hoc tests (Appendix S2, S5, S7).

Regional dynamics

On the regional scale, absolute and relative *L. polyedra* biovolume reflected local dynamics. Both were overall relatively low and did not reveal strong differences between the different inoculation times and positions.

Generally, both early inoculation treatments, $Start_{one}$ and $Start_{five}$, showed a strong increase in absolute *L. polyedra* biovolume until day nine, with a stronger increase in the $Start_{one}$ treatment. In both treatments ($Start_{one}$, $Start_{five}$) *L. polyedra* biovolume decreased after nine days, resulting in similar *L. polyedra* biovolume in both treatments at day 24 (Fig.9). In the $Late_{one}$ treatment, *L. polyedra* biovolume slightly increased until day 18 and remained relatively constant after that (Fig.9), whereas it only increased in the $Late_{five}$ treatment until day 12, after which it slightly decreased again. However, *L. polyedra* biovolume was still relatively similar in both treatments. Hence, the results of the linear mixed models from day 15 until the end of the experiment, as well as the ANOVA results after similar incubation times (day nine and 15 of the 'early' treatment, day 18 and 24 of the 'late' treatment) showed no treatment effects on the regional, absolute *L. polyedra* biovolume (Tab. 4, 5).

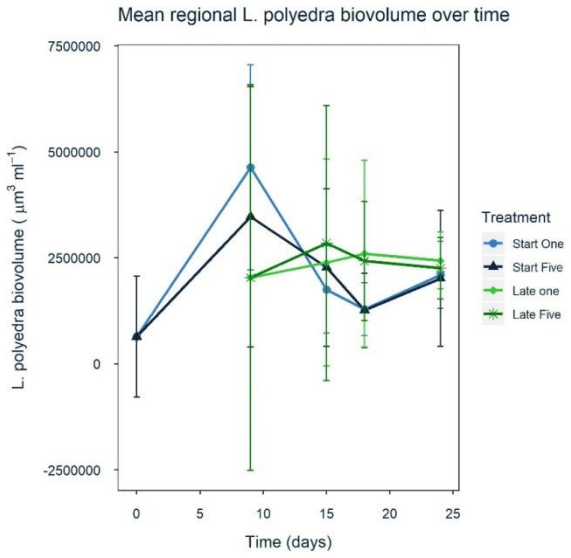


Figure 9 Mean regional L. polyedra biovolume ± SD ($\mu m^3\ ml^{-1}$) over time. Regional means were calculated from the mean of all five flasks of one meta-ecosystem. L. polyedra inoculation treatments ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$) are represented by different colors.

Table 6 Results from linear mixed models of the local community, testing the effect of different treatments ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$, Control) and the position along the nutrient gradient, as well as their interacion for responses of particulate nutrient ratios (A-C) for the last day of the experiment (day 24).
*Degree of freedom, F-values and p-values are shown. Significant effects are highlighted bold. C:N and C:P ratios were log transformed. [*1] refers to corresponding post-hoc pairwise comparison results in the appendix: S12.*

		Factor	df	F	p
A	(log) C:N ratio	Treatment	4	5.854	***<0,001*** [*1]
		Position	1	72.195	***<0,001***
		Treatment : Position	4	1.576	0.194
B	(log) C:P ratio	Treatment	4	0.599	0.665
		Position	1	11.701	***<0,01***
		Treatment : Position	4	0.373	0.827
C	N:P ratio	Treatment	4	0.815	0.521
		Position	1	0.817	0.370
		Treatment : Position	4	0.601	0.664

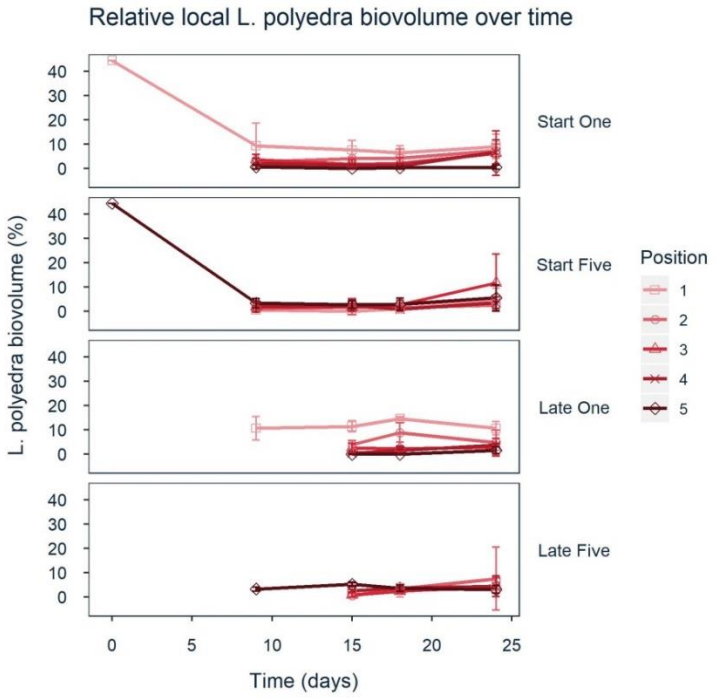


Figure 10 *Mean local L. polyedra biovolume contribution ± SD (% of the total phytoplankton biovolume) over time. Plots are split up into L. polyedra inoculation treatments ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$). Colors indicate the increasing nutrient concentration in the respective position from light (position 1) to dark red (position 5).*

The early inoculation overall resulted in a slight decrease of the relative *L. polyedra* biovolume contributions, with a minor recovery towards the end of the experiment (Fig.11). The late inoculation of *L. polyedra*, in contrast, led to a slow increase in its contribution. However, relative *L. polyedra* biovolume contributions were only significantly different, after nine days of incubation (day nine of the 'early' treatment, day 18 of the 'late' treatment; ($p<0.05$, Tab. 5a), were *L. polyedra* contributions were generally higher in the late inoculation treatments and when inoculated at low nutrient concentrations. However, relative *L. polyedra* contributions were only significantly higher in the $Late_{one}$ treatment compared to the $Start_{five}$ treatment (Tukey's HSD, $p<0.05$, Appendix S10).

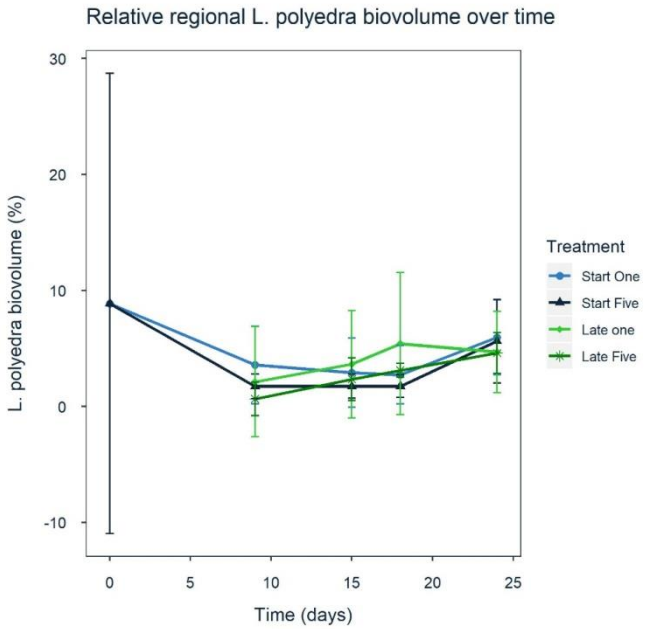


Figure 11 Mean regional *L. polyedra* biovolume contribution ± SD (% of the total phytoplankton biovolume). Regional means were calculated from the mean of all five flasks of one meta-ecosystem. *L. polyedra* inoculation treatments ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$) are represented by different colors.

Nutrient dynamics

Dissolved nutrients

The step-wise increase in nutrient concentration from medium 1 to medium 5 (Tab. 1) along the nutrient gradient in the meta-ecosystems could be maintained over the first six to nine days of the experiment (Fig. 12, 13). Dissolved N and P decreased quickly in all positions and independent of the different inoculation treatments. Nitrogen decreased quickly until day

nine, after which it remained below 1µmol L^{-1} in all positions and treatments, and even below 0.5µmol L^{-1} between day 12 and 21 (Fig. 12). Phosphorus decreased faster than N and reached low concentrations already at day six (Fig. 13). However, remaining levels were higher and varied between 0.24 - 1.5µmol L^{-1} (position 1) and 0,24 – 2.62 µmol L^{-1} (position 5).

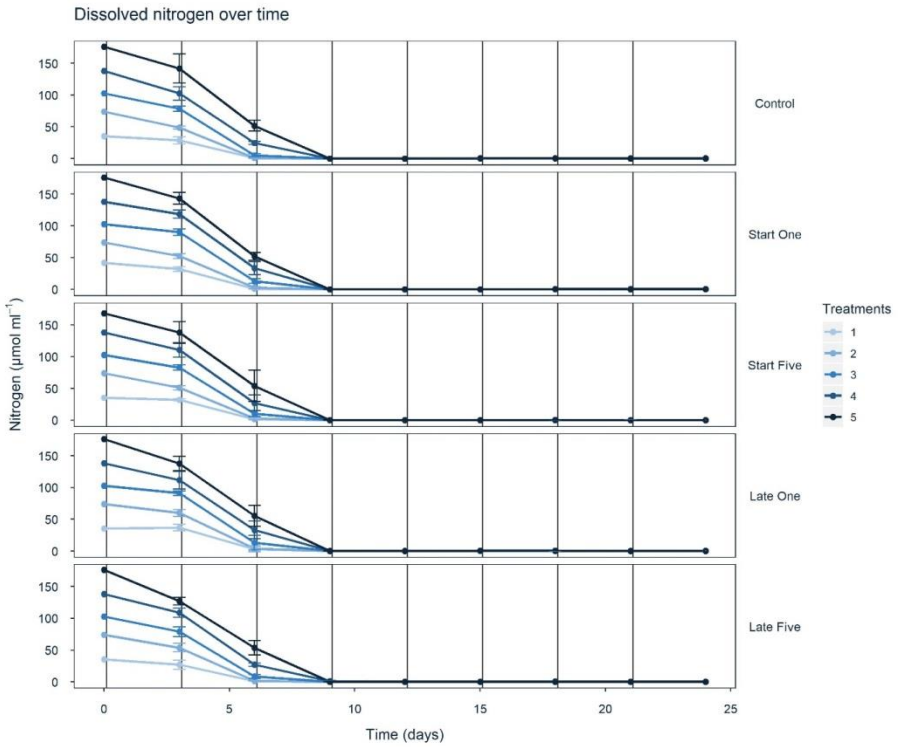


Figure 12

Mean dissolved nitrogen ± SD (µmol ml^{-1}) over time. Plots are split up into L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$). Colors indicate the increasing nutrient concentration in the respective position from light (position 1) to dark blue (position 5). Vertical lines indicate semi-continuously introduction of N and P.

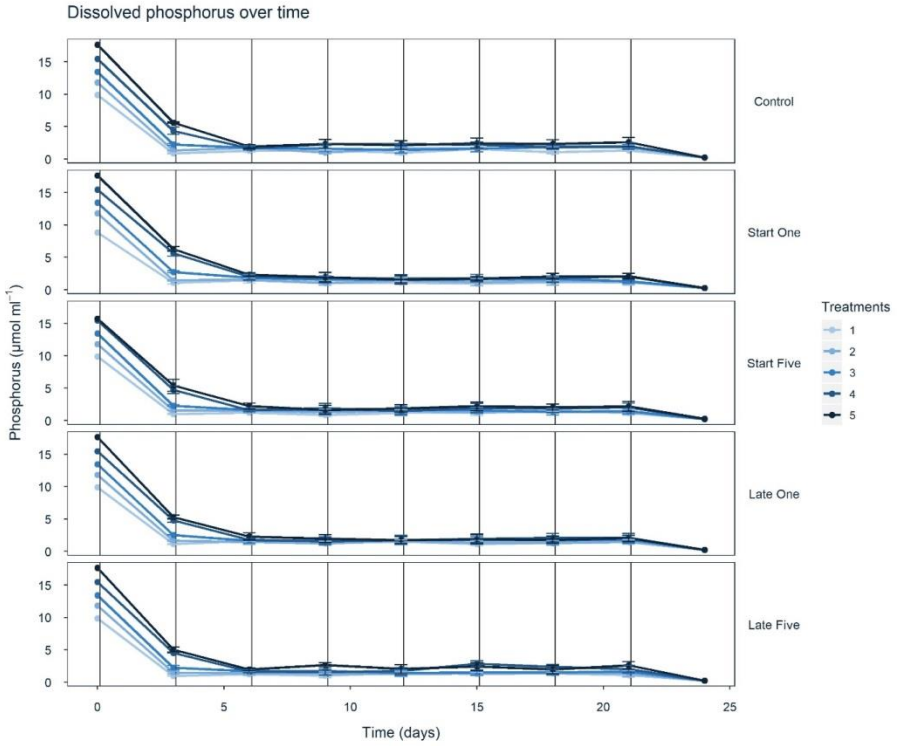


Figure 13

Mean dissolved phosphorous ± SD (µmol ml^{-1}) over time. Plots are split up into L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$). Colors indicate the increasing nutrient concentration in the respective position from light (position 1) to dark blue (position 5). Vertical lines indicate semi-continuously introduction of N and P.

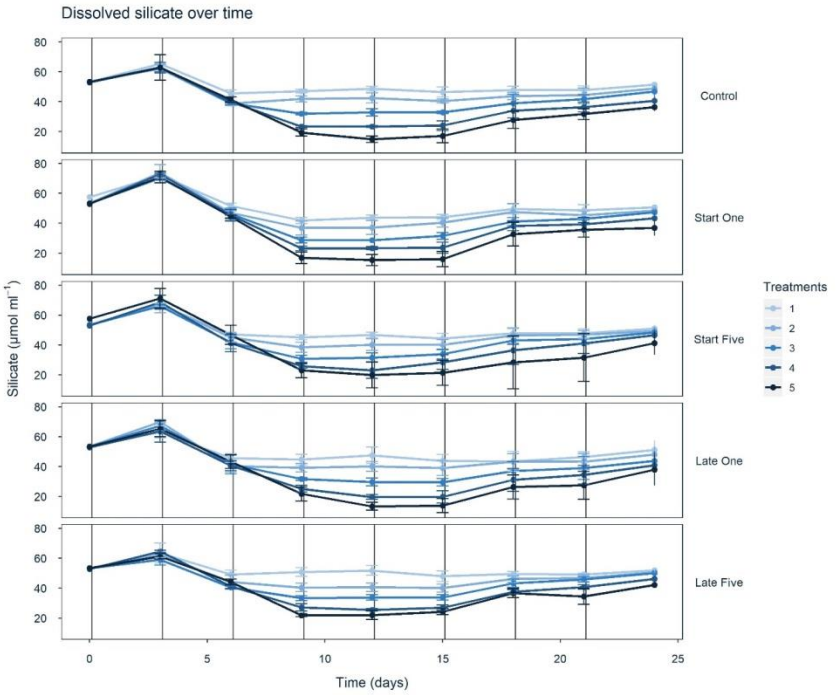


Figure 14

Mean dissolved silicate ± SD (µmol ml^{-1}) over time. Plots are split up into L. polyedra inoculation treatments (Control, Start$_{one}$, Start$_{five}$, Late$_{one}$, Late$_{five}$). Colors indicate the position along the nutrient gradient. Vertical lines indicate semi-continuously introduction of N and P. Silicate was not added with the nutrient input.

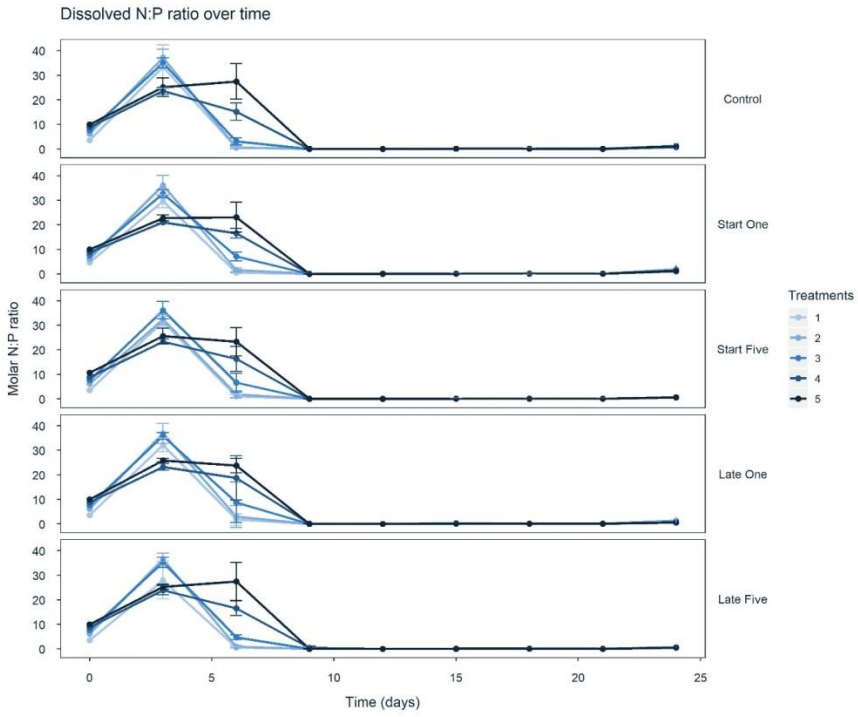


Figure 15

Mean molar dissolved N:P ratios ± SD over time. Plots are split up into L. polyedra inoculation treatments (Control, Start$_{one}$, Start$_{five}$, Late$_{one}$, Late$_{five}$). Colors indicate the increasing nutrient concentration in the respective position from light (position 1) to dark blue (position 5).

Silicate was not manipulated due to the high initial concentration in the natural seawater used to prepare the different growth media. Dissolved silicate was consumed in all flasks. However, the reduction was stronger in the highest nutrient positions, where diatoms were dominating most strongly (Fig. 14). No difference of the inoculation position and timing of *L. polyedra* was observed for dissolved Si. Concentrations of Si were lowest between day nine and fifteen, after which they slightly increased in higher positions while remaining stable in position 1. Between

day 18 and 24, Si concentrations remained stable and varied between 7.99 µmol L^{-1} and 57,64 µmol L^{-1}, with lower concentrations at higher positions and vice versa.

Dissolved N:P ratios showed a hump-shaped distribution between the beginning of the experiment and day nine, after which they decreased to almost zero (Fig. 15), indicating a strong N limitation. The initial increase in N:P represented the faster decline of phosphorus compared to nitrogen. The subsequent decline of the dissolved N:P ratio represented the reduction of dissolved nitrogen, after which phosphorus concentrations were already depleted. Higher nutrient concentrations (position 4 and 5) showed a lower and slower increase of the N:P ratio, followed by a shifted decrease (Fig. 15). The observed pattern was found for all treatments.

Particulate nutrients

Particulate N, P and carbon (C) were measured at the beginning of the experiment, before the late inoculation of *L. polyedra* (only in the control without *L. polyedra*), as well as the at the last day of the experiment. On the last day of the experiment particulate nutrients reflected the nutrient gradient as they increased with increasing dissolved nutrient concentrations (Appendix S19 - 21). In all treatments, increasing nutrient concentrations also increased the amount of nutrient per carbon. Thus, at day 24 C:N and C:P ratios were significantly lower with increasing nutrient concentration along the meta-ecosystem ($p<0.01$; Tab. 6, Fig. 16, 17).

Initial particulate carbon to nutrient ratios, i.e. C:N and C:P ratios, as well as N:P ratios were slightly lower in flasks where *L. polyedra* was added. However, this difference was not observed at the end of the experiment. Overall, C:N and C:P ratios increased in all positions and all treatments from the beginning to the last day of the experiment (Appendix S22&23). However, particulate nutrients were also measured for the control at day nine (the inoculation day of the $Late_{one}$ and $Late_{five}$ treatment), which showed an even stronger increase of the C:N ratio at that day. Thus, C:N ratios of the $Late_{one}$ and $Late_{five}$ treatment increased from the beginning of the experiment until day nine, after which they decreased until day 24 (Appendix S22). C:P ratios also increased from day zero to day nine, however ratios between day nine and 24 in position 2-5 along the nutrient gradient remained relatively stable. However, C:P ratios at position one where much higher at day nine, and thus decreased until day 24. At the last day of the experiment, the local C:N ratio was significantly influenced by the inoculation treatments ($p<0.001$; Tab. 6), with significantly higher ratios in the $Start_{five}$ and $Late_{one}$

treatments compared to the control and the $Start_{one}$ treatment ($p<0.05$; Appendix S12). Similar results were found on the regional scale, with significant differences between the same treatments ($p<0.1$; Tab. 7, Appendix S13). Only the difference between the $Late_{one}$ and $Start_{one}$ treatment was just above the significance threshold on the regional scale ($p<0.0522$; Appendix S12). The increased C:N ratios of the $Late_{one}$ treatment can be ascribed to increased carbon concentrations, while the $Start_{five}$ treatment exhibited increased carbon and decreased nitrogen concentrations, resulting in the elevated C:N ratio.

Local and regional particulate N:P ratios remained similar between day 0, 9 and day 24, with only two exceptions for the local $Start_{one}$ and $Start_{five}$ treatment at day 24 in position 4, as well as at day nine in position 1, which both had a higher N:P ratio (Appendix S24). However, analyses for day 24, showed no significant effects from the position, i.e. the nutrient gradient, nor from the inoculation treatment on the N:P ratios (Tab. 6, Fig. 18).

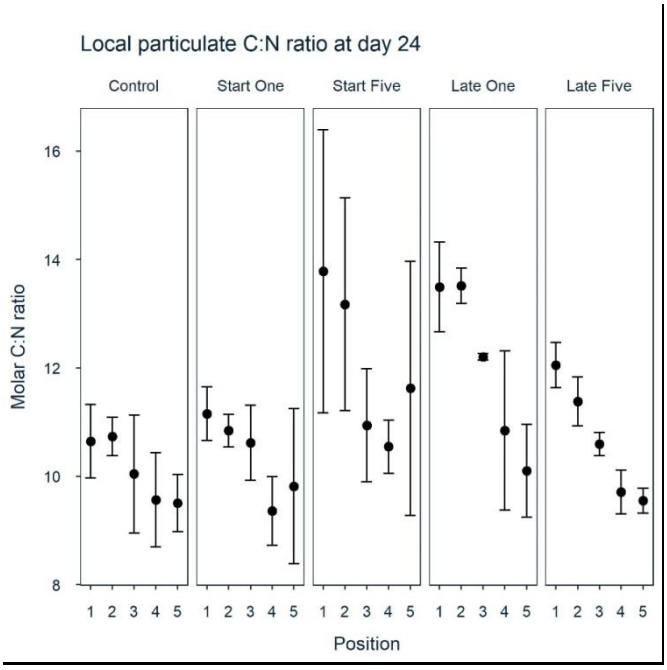


Figure 16 *Mean molar particulate C:N ratios ± SD at the end of the experiment (day 24) over the position along the nutrient gradient (increasing nutrient concentrations from position 1-5. Plots are split up into L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$).*

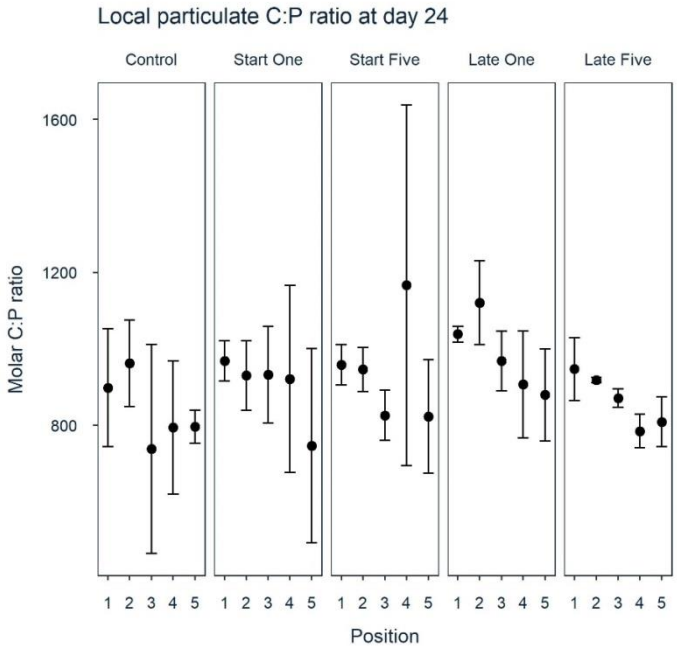


Figure 17 *Mean molar particulate C:P ratios ± SD at the end of the experiment (day 24) over the position along the nutrient gradient (increasing nutrient concentrations from position 1-5). Plots are split up into L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$).*

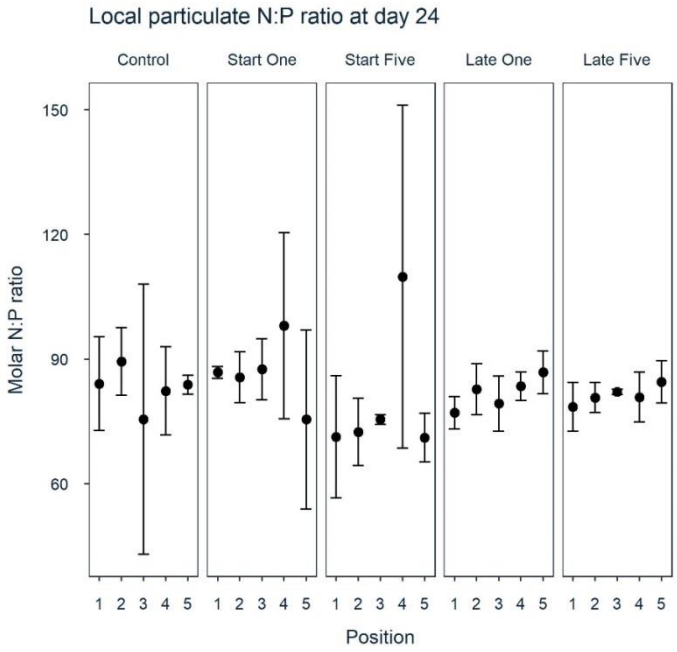


Figure 18 Mean molar particulate N:P ratios ± SD at the end of the experiment (day 24) over the position along the nutrient gradient (increasing nutrient concentrations from position 1-5). Plots are split up into *L. polyedra* inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$).

Table 7 Results from linear mixed models of the regional community, testing the effect of different treatments ($Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$, Control) for responses of particulate nutrient ratios (A-C) for the last day of the experiment (day 24).
Regional responses were calculated by the mean of all five flasks of one meta-ecosystem. Degree of freedom, Sum of squares, Mean squares, F-values and p-values are shown. Significant effects are highlighted bold. *1 refers to corresponding post-hoc test results (Tukey's HSD) in the appendix: S13.

		Factor	df	Sum Sq	Mean Sq	F value	p
A	CN ratio	Treatment	4	10.943	2.736	6.92	***<0,01*** *1
		Residuals	10	3.953	0.395		
B	NP ratio	Treatment	4	61.3	15.32	0.244	0.907
		Residuals	10	628.7	62.87		
C	CP ratio	Treatment	4	46887	11722	1.199	0.37
		Residuals	10	97797	9780		

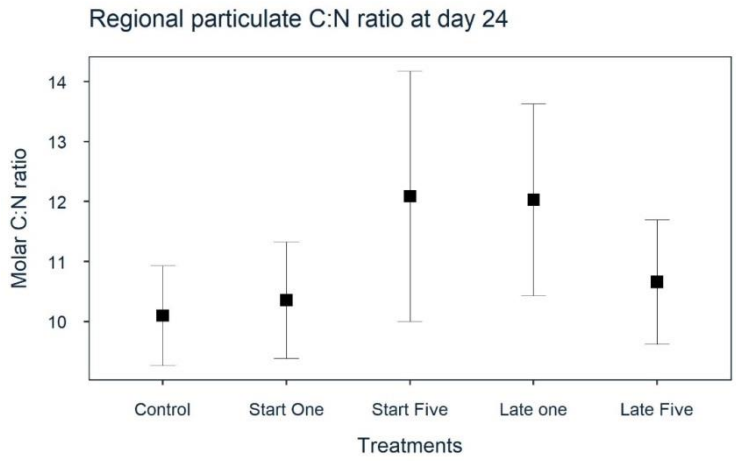


Figure 19 *Mean regional molar particulate C:N ratios ± SD at the end of the experiment (day 24). Regional means were calculated from the mean molar particulate C:N ratios of all five flasks of one meta-ecosystem. Plot includes all L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$).*

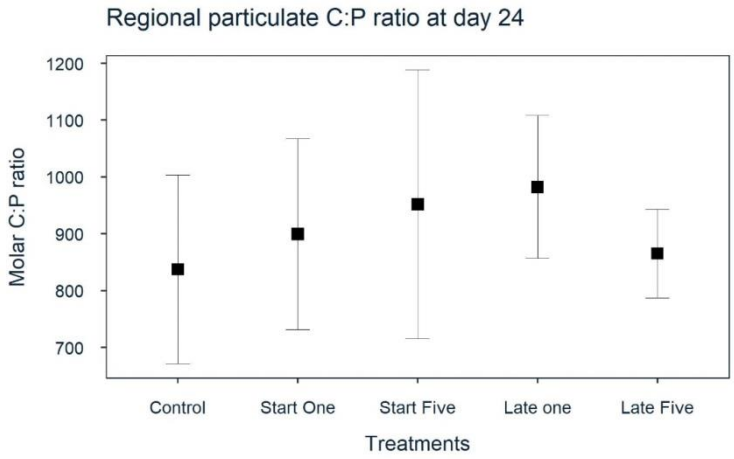


Figure 20 *Mean regional molar particulate C:P ratios ± SD at the end of the experiment (day 24). Regional means were calculated from the mean molar particulate C:P ratios of all five flasks of one meta-ecosystem. Plot includes all L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$).*

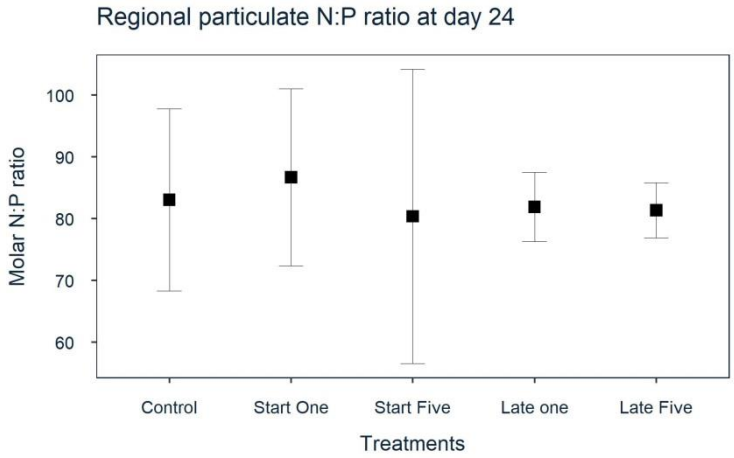


Figure 21 *Mean regional molar particulate N:P ratios ± SD at the end of the experiment (day 24). Regional means were calculated from the mean molar particulate N:P ratios of all five flasks of one meta-ecosystem. Plot includes all L. polyedra inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$).*

Discussion

Overall, *L. polyedra* exhibited higher relative biovolume contributions at lower nutrient concentrations, especially when inoculated into this position, indicating, that both the nutrient concentrations, as well as the inoculation position play an important role for *L. polyedra* dynamics. However, it did not form a bloom, independent of the inoculation time and positioning in the meta-ecosystem. Even with an initial biomass advantage, when it was

inoculated in the beginning, *L. polyedra* was not able to maintain its prevalent position in the community and thus did not dominate the community at any further time point during the experiment. Communities along the nutrient gradient were stimulated by the nutrient supply, and thus increased their biomass and decreased evenness with increasing nutrient availability.

Species interactions and L. polyedra dynamics

In this experiment, both diatom and both dinoflagellate species showed similar responses, with higher dinoflagellate contributions at lower nutrient concentrations. Overall, however, community dynamics mostly represented changes in the diatom biomass, as they were by far the most dominant group in all meta-ecosystem positions. Dinoflagellates contributed higher biomass under low nutrient conditions compared to higher nutrients, as well as marginal higher relative proportions at later time points in the experiment, when diatom contributions decreased due to the depletion of nutrients.

The timing of the inoculation of *L. polyedra* had no significant influence on *L. polyedra* abundance, still, it showed that absolute growth was stronger when inoculated at the beginning, when nutrients were still high, whereas growth was weaker, when inoculated after nine days. However, the initial relative proportion of *L. polyedra* was much higher (>40%), when inoculated at the beginning, which might have promoted initial growth more, compared to the later inoculations, where growth after the inoculation was weaker. In this meta-ecosystem experiment all cells, including *L. polyedra* cells, were able to disperse between patches of different nutrient conditions, providing different habitats and potential niches. *L. polyedra* was hence able to get established in all positions along the nutrient gradient, even though with low biomass contributions only. Independent of the inoculation position and timing, *L. polyedra* biomass in all treatments became more similar towards the end. This might indicate a homogenization of the communities through dispersal of cells and nutrients as well as a balance of growth through recycled and newly introduced nutrients and regular removal of cells through sampling, thus resulting in a steady state.

While absolute biomass of *L. polyedra* was relatively low in all positions along the nutrient gradient, relative proportions showed more distinct differences between positions. *L. polyedra* relative contributions increased with decreasing nutrient concentrations, especially when inoculated under lowest nutrient conditions. In a study on the Western Mediterranean Sea, Mercado et al. (2014) observed that changes in relative dinoflagellate contributions were mostly caused by changes in diatom abundances over an increasing nutrient gradient towards the coast. This effect can also be seen in the results of this experiment, as under lower nutrient conditions, lower diatom abundances promoted higher relative dinoflagellate contributions. Hence, relative biovolume differences of *L. polyedra* can not only be ascribed to differences in its inoculation position and timing, but also to differences in community succession, mostly driven by diatoms, which grew in high dependency of nutrient availability.

In contrast to the study of Mercado et al. (2014), however, relative *L. polyedra* contributions only increased very little after the decay of the diatom bloom, and could by far not exceed diatom dominance. Still, in this experiment, *L. polyedra* was a better competitor under low-nutrient conditions. Different studies have shown that some dinoflagellates can store inorganic nitrogen (Collos et al., 2004; Dagenais-Bellefeuille and Morse, 2013; Maguer et al., 2007), providing a competitive advantage under low nutrient conditions in dynamic systems. In my experiment, *L. polyedra* grew better when it was inoculated at the beginning when inorganic nutrients were still available. Taking this into account, it is possible that *L. polyedra* stored nitrogen when it was still available and could, therefore, grow and maintain its population under low nutrient conditions, while diatom biomass was lower in comparison to higher nutrient levels. However, it remains unclear, if *L. polyedra* can store nitrogen sufficiently for growth, as Dagenais-Bellefeuille et al. (2014) showed, that under nitrogen stress, cell growth of *L. polyedra* stopped.

Additionally, mixotrophic feeding on bacteria or other phytoplankton species could have promoted growth of *L. polyedra.* Especially under lower nutrient conditions, where nutrient availability was low from the beginning on, such ingestion could explain the comparably “well” performance under low nutrient conditions compared to higher nutrient positions. The same strain of *L. polyedra* had been shown to exhibit an enhanced phagotrophic feeding on the picoplankton *Ostreococcus* sp. under nitrogen as well as nitrogen and phosphorus depletion (Busch, 2016). However, while mixotrophic feeding of *L. polyedra* has been demonstrated for

a variety of groups, such as bacteria, cyanobacteria, dinoflagellates and diatoms (Jeong et al., 2005b; Seong et al., 2006; Yoo et al., 2009; Zhang et al., 2013), it has not specifically been tested for the community species of this experiment.

Despite higher contributions under lower nutrient conditions, *L. polyedra* was overall an inferior competitor, and its impact remained low throughout this meta-ecosystem experiment. In nature, *L. polyedra* has been shown to produce massive blooms, with often more than 1 Mio cells L^{-1} (e.g. Allen 1946; Holmes, Williams, and Eppley 1967; Bruno et al. 1990), raising the question, why *L. polyedra* could not thrive in this experimental setup.

Overall, it is very likely that diatoms hampered dinoflagellate growth, as they represented the stronger competitors for nutrients during the experiment. Strong competitive interactions of dinoflagellates and diatoms are a common phenomenon in nature, especially in fluctuating systems, such as upwelling regions. Under high nutrient and turbulent conditions, diatoms often bloom, whereas dinoflagellates thrive under lower nutrient, but also calmer conditions (Margalef, 1978). On the Namaqua shelf of the Benguela upwelling system, for instance, such a phytoplankton succession from fast-growing diatoms to motile dinoflagellates has been found according to changes from a well-mixed and nutrient-rich to a stratified nutrient-poor environment (Pitcher and Nelson, 2006). Anderson et al. (2008) showed a similar pattern for the Santa Barbara Channel in the Southern California Bight, where they found a distinct set of conditions leading to diatom (upwelling-driven) or dinoflagellate (promoted by stratification) blooms, including differences in temperature, stratification and nutrients. But also other regions than upwelling systems are prone to exhibit a succession from diatom to dinoflagellate blooms when nutrients get depleted. For example, in Georges Bank in the Gulf of Maine (Gettings et al., 2014) or the Bornholm Basin in the Baltic Sea (van Beusekom et al., 2009), dinoflagellates showed distinct successions after the decrease of diatom bloom events through decreased nutrient concentrations and increased stratification. In my experiment, diatom performance resembled field observations of high biomass blooms at high nutrient concentrations. However, despite the decrease of diatom biomass after their intense bloom, most likely due to decreased nitrogen and phosphorus, a succession towards a dinoflagellate bloom did not occur. Hence, changes in nutrient concentrations might have been less

important than other factors, such as spatially different niches, which occur under stratified conditions.

While the horizontal movement was possible, flask size was very limited and thus vertical migration could not be considered in this experiment. Different studies have, however, reported, that *L. polyedra* can migrate vertically (Eppley et al., 1968; Heaney and Eppley, 1981; Moorthi et al., 2006). Vertical migration could thus enhance bloom onset, as it was shown to be a strategy of predator avoidance and nutrient uptake in deeper nutrient-rich waters (Bollens et al., 2012; Eppley and Harrison, 1975). Mann (1992) reported that diatom growth was mostly promoted under turbulent conditions because mixing prevented diatom cells from sinking, whereas dinoflagellate could endure under stratified conditions through their motility, which enabled them to migrate into deeper, nutrient-rich waters. Especially in the light of strong competitive interactions, dial migration in a stratified environment could enhance bloom formation of *L. polyedra* in the field.

The results of this experiment show that the community composition of coexisting species is highly important for *L. polyedra* performance, for instance, the presence and abundance of diatoms. Hence, dynamics in natural systems might differ from such a simplified laboratory experiment, as natural plankton communities represent more complex systems compared to the community used in this experiment. Additionally, successional states of communities might still be important for their responses to nutrient inputs.

Grazing plays an important role in natural plankton communities. Grazing by zooplankton, but also other mixotrophs can both, terminate phytoplankton blooms through direct grazing and also promote blooms, through feeding on potential competitors, and thus indirectly enhance other species (Buskey, 2008; Smayda, 2002; Sunda et al., 2006). Thus, blooms of *L. polyedra* might be promoted by a combination of factors, which were not included in this experiment, as dissolved nutrients as a single factor only did not promote its blooms. Therefore, more research on the interactions of nutrients and phytoplankton community composition on the bloom performance of *L. polyedra* needs to be done.

Nutrient dynamics

Dissolved nutrients reflected the strong initial phytoplankton growth at the beginning of the experiment, which quickly decreased nitrogen and phosphorus in all positions. Increasing diatom growth with increasing dissolved nutrient concentrations also led to a stronger decrease of dissolved silicate with increasing position along the nutrient gradient. Despite the decrease of dissolved Si in all positions, from day 15 on, it increased again, probably due to chemical remineralisation processes (DeMaster, 1981; Dugdale and Wilkerson, 2001).

Particulate nutrients from the last day of the experiment represented the internal nutrient composition of the algal community. Already Redfield described the molar internal nutrient ratio of 106:16:1 (C:N:P) for unlimited nutrient conditions in marine phytoplankton (Redfield, 1934). These ratios play an important role in the ecological stoichiometry (ES), which considers the balance between chemical substances in ecological interactions and processes (Sterner and Elser, 2002). Such a concept helps to understand ecological interactions within food webs, as primary producers, compared to heterotrophs, are generally more flexible in their elemental composition which thus affects their quality as a food source (Elser et al., 2000; Finkel et al., 2010; McIntyre and Flecker, 2010; Moorthi et al., 2017; Persson et al., 2010; Sterner and Elser, 2002). However, mixotrophic organisms, such as dinoflagellates, might be less affected by these imbalances, as they can potentially compensate for the nutrient limitations through feeding on nutrient-rich prey organisms (Moorthi et al., 2017).

Despite the stepwise increase of the nutrient concentration, fairly constant particulate N:P ratios along the nutrient gradient and from day 0 to day 24 reflected the consistent ratios of dissolved nutrients in the medium. In contrast to the beginning, however, increased particulate C:N and C:P ratios were found, indicating limited nutrient conditions, as the ratios reflected a high C fixation, but low nutrient conditions, which would also be in agreement, with the depleted dissolved nutrients. According to the theory of ES, phytoplankton C: nutrient ratios increased with decreasing nutrient supply, i.e. increasing nutrient limitation (Elser et al., 2000; Moorthi et al., 2016; Sterner and Elser, 2002). Thus, the communities would be of increasing food quality with increasing nutrient concentration, as lower C to nutrient ratios of phytoplankton generally provide higher quality food for consumers (e.g. Elser, Hayakawa and Urabe, 2001; Moorthi et al., 2016).

I found significant differences in the C:N ratios between different inoculation treatments, mostly due to changes in carbon concentrations. However, neither species composition,

biomass nor other measured factors on the last day of the experiment can explain these differences. Garcia et al. (2018) observed a high variability of cellular elemental stoichiometry (C:N:P) within isolates of different phytoplankton classes, with higher C:N ratios in dinophyceae, compared to bacillariophyceae. As dinoflagellates had a stronger influence on the total biomass in lower nutrient concentrations in my experiment, higher C:N ratios of dinoflagellates could have supported the shift from high to low C:N content along the nutrient gradient. However, Moorthi et al. (2017) showed, that the mean and variance of internal C:P ratios of phytoplankton communities decreased with increasing contributions of mixotrophic phytoplankton (including dinophyta) in samples from two natural lake surveys. Particulate C to nutrient ratios in my experiment represented the internal nutrient composition of the entire community. Hence it is highly speculative to draw any conclusions for specific species in this experiment.

Spatial properties and dispersal

Meta-ecosystem studies provide the opportunity to study spatial interactions of organisms in combination with the spatial flow of energy or material, such in this experiment the spatial flow of nutrients (Loreau et al., 2003). In my experiment, *L. polyedra* cells appeared in all flasks, independent of the inoculation position, thus showing, that dispersal in both directions along the nutrient gradient was possible. However, while the general influence of *L. polyedra* was low, inoculation position still influenced local dynamics of *L. polyedra.* Thus, inoculation position, as well as the transportation of cells plays an important role for population dynamics on a spatial scale.

Dispersal has been shown to be an important factor for bloom propagation, whereas bloom formation depended on local environmental conditions (Bialonski et al., 2016). However, dispersal can also weaken bloom formation, as demonstrated in the meta-ecosystem experiment described in Chapter 1, where the dominance of *A. catenella* was much stronger under lowest nutrient concentrations without dispersal, probably due to the lack of patch homogenization. Hence, it is possible, that *L. polyedra* would have performed better without or with a lower rate of dispersal.

The meta-ecosystems were placed on a shaking table, to allow all species to disperse between patches of different nutrient concentrations. An intermediate shaking speed also allowed non-

motile species to disperse along the nutrient gradient, but also accounted for the maintenance of the nutrient gradient. Different studies have shown that dinoflagellates, including *L. polyedra,* occur in calmer waters, often after mixing events in upwelling (Kudela et al., 2005; Langlois and Smith, 2001; Margalef, 1978). In this experiment, especially when inoculated early, the regional abundance of *L. polyedra* initially increased, thus providing evidence, that water movement in this set-up was not the crucial factor hindering bloom formation. However, I cannot exclude, that it might have negatively affected *L. polyedra* performance.

Conclusion

Overall, the results of this study show a strong competitive interaction between diatoms and dinoflagellates, where diatoms were able to take the lead. Diatoms were able to dominate all communities independent of the nutrient concentration and the inoculation position or timing of *L. polyedra*. However, the dinoflagellate *L. polyedra* was a better competitor under lower nutrient concentrations and performed better when inoculated into this position. My results indicate, that nutrient input and phytoplankton community composition, their successional state and thus competition between species, are important determinants for bloom dynamics of this harmful dinoflagellates.

L. polyedra naturally occurs in upwelling systems, where nutrients are highly dynamic and strongly determine competitive interactions with diatoms and other algae. While the timing of the inoculation of *L. polyedra* had only minor influences on its bloom dynamics in this experiment, temporal aspects of nutrient availability, i.e. the timing of nutrient pulses may play a more important role for these interactions. As upwelling is not a constant process, but rather occurs in pulses, a promising next step would be to study the effects of the timing of nutrient pulses in combination with the effects of community composition on *L. polyedra* in order to enhance our understanding of its bloom dynamics in upwelling systems.

Appendix

Appendix S1 Results from the post-hoc comparison of the linear mixed model for *L. polyedra* biovolume calculated from day 15 until the end of the experiment. *L. polyedra* biovolume was square root transformed. p-values were adjusted after Tukey.

```
lm_lingulo<- lmer(sqrt(lingulo_bv)~ treat*pos
              +(1|no_unit)
              +(1|time)
              ,data=data_ling)

emmeans(lm_lingulo, pairwise~treat,type = "response")

$emmeans
 treat response       SE df  lower.CL upper.CL
 LSO    1197913 326777.6  8  562868.6  2069970
 LSF    1113695 315081.4  8  505621.9  1958780
 LLO    1706205 389991.5  8  925388.4  2724033
 LLF    1862702 407484.7  8 1041546.7  2920870

Degrees-of-freedom method: satterthwaite
Confidence level used: 0.95
Intervals are back-transformed from the sqrt scale

$contrasts
 contrast    estimate       SE df t.ratio p.value
 LSO - LSF   39.17474 211.1177  8   0.186  0.9975
 LSO - LLO -211.72542 211.1177  8  -1.003  0.7523
 LSO - LLF -270.31624 211.1177  8  -1.280  0.5986
 LSF - LLO -250.90016 211.1177  8  -1.188  0.6501
 LSF - LLF -309.49098 211.1177  8  -1.466  0.4978
 LLO - LLF  -58.59082 211.1177  8  -0.278  0.9920

P value adjustment: tukey method for comparing a family of 4 estimates
```

Appendix S2 Results from the post-hoc comparison of the linear mixed model for relative *L. polyedra* biovolume calculated from day 15 until the end of the experiment. Relative *L. polyedra* biovolume was square root transformed. p-values were adjusted after Tukey.

```
lm_lingu_perc<- lmer(sqrt(perc_lingulo)~ treat*pos
                +(1|no_unit)
                +(1|time)
                ,data=data_ling)
emmeans(lm_lingu_perc, pairwise~treat,type = "response")

$emmeans
 treat response        SE   df  lower.CL upper.CL
 LSO   2.441232 0.9715782 7.46 0.6995535 5.237210
 LSF   1.800606 0.8344161 7.46 0.3792290 4.276284
 LLO   2.898050 1.0585862 7.46 0.9531910 5.897209
 LLF   2.515097 0.9861674 7.46 0.7393500 5.345144

Degrees-of-freedom method: satterthwaite
Confidence level used: 0.95
Intervals are back-transformed from the sqrt scale

$contrasts
 contrast     estimate      SE df t.ratio p.value
 LSO - LSF  0.22057742 0.34898  8   0.632  0.9188
 LSO - LLO -0.13992186 0.34898  8  -0.401  0.9767
 LSO - LLF -0.02346152 0.34898  8  -0.067  0.9999
 LSF - LLO -0.36049928 0.34898  8  -1.033  0.7361
 LSF - LLF -0.24403894 0.34898  8  -0.699  0.8946
 LLO - LLF  0.11646035 0.34898  8   0.334  0.9862

P value adjustment: tukey method for comparing a family of 4 estimates
```

Appendix S3 *Results from the post-hoc comparison of the linear mixed model for L. polyedra biovolume calculated for 9 days after L. polyedra inoculation. Relative L. polyedra biovolume was square root transformed. p-values were adjusted after Tukey*

```
lm_eve_9<- lmer(evenness~ treat*pos
                    +(1|no_unit)
                    ,data=temp_data_9)
emmeans(lm_eve_9, pairwise~treat,type = "response")

$emmeans
 treat response        SE df lower.CL upper.CL
 LLF   2.795513 0.6831829  8 1.442049 4.592894
 LLO   3.352544 0.7481582  8 1.849247 5.299759
 LSF   1.194378 0.4465572  8 0.386574 2.446100
 LSO   2.363419 0.6281692  8 1.136818 4.033939

Degrees-of-freedom method: satterthwaite
Confidence level used: 0.95
Intervals are back-transformed from the sqrt scale

$contrasts
 contrast    estimate        SE df t.ratio p.value
 LLF - LLO -0.1590166 0.2889291  8  -0.550  0.9439
 LLF - LSF  0.5791027 0.2889291  8   2.004  0.2626
 LLF - LSO  0.1346370 0.2889291  8   0.466  0.9645
 LLO - LSF  0.7381193 0.2889291  8   2.555  0.1246
 LLO - LSO  0.2936536 0.2889291  8   1.016  0.7451
 LSF - LSO -0.4444657 0.2889291  8  -1.538  0.4605

P value adjustment: tukey method for comparing a family of 4 estimates
```

Appendix S4 Results from the post-hoc comparison of the linear mixed model for *L. polyedra* biovolume calculated for 9 days after *L. polyedra* inoculation. Relative *L. polyedra* biovolume was square root transformed. p-values were adjusted after Tukey

```
lm_ling_9<- lmer(sqrt(lingulo_bv)~ treat*pos
                 +(1|no_unit)
                 ,data=temp_data_9)

emmeans(lm_ling_9, pairwise~treat,type = "response")

$emmeans
 treat response       SE df  lower.CL upper.CL
 LLF    2059241 693696.7  8  770238.7  3969574
 LLO    1770220 643175.7  8  597718.9  3564051
 LSF    2240532 723588.5  8  882599.4  4219795
 LSO    3321286 880986.3  8 1600393.0  5663509

Degrees-of-freedom method: satterthwaite
Confidence level used: 0.95
Intervals are back-transformed from the sqrt scale

$contrasts
 contrast    estimate       SE df t.ratio p.value
 LLF - LLO  104.50962 341.8228  8   0.306  0.9893
 LLF - LSF  -61.83514 341.8228  8  -0.181  0.9977
 LLF - LSO -387.43395 341.8228  8  -1.133  0.6809
 LLO - LSF -166.34476 341.8228  8  -0.487  0.9599
 LLO - LSO -491.94358 341.8228  8  -1.439  0.5119
 LSF - LSO -325.59881 341.8228  8  -0.953  0.7788

P value adjustment: tukey method for comparing a family of 4 estimates
```

Appendix S5 Results from the post-hoc comparison of the linear mixed model for relative *L. polyedra* biovolume calculated for 9 days after *L. polyedra* inoculation. Relative *L. polyedra* biovolume was square root transformed. p-values were adjusted after Tukey

```
lm_percling_9<- lmer(sqrt(perc_lingulo)~ treat*pos
                 +(1|no_unit)
                 ,data=temp_data_9)

emmeans(lm_percling_9, pairwise~treat,type = "response")#no pairwise sign

$emmeans
 treat response        SE df lower.CL upper.CL
 LLF   2.795513 0.6831829  8 1.442049 4.592894
 LLO   3.352544 0.7481582  8 1.849247 5.299759
 LSF   1.194378 0.4465572  8 0.386574 2.446100
 LSO   2.363419 0.6281692  8 1.136818 4.033939

Degrees-of-freedom method: satterthwaite
Confidence level used: 0.95
Intervals are back-transformed from the sqrt scale

$contrasts
 contrast    estimate        SE df t.ratio p.value
 LLF - LLO -0.1590166 0.2889291  8  -0.550  0.9439
 LLF - LSF  0.5791027 0.2889291  8   2.004  0.2626
 LLF - LSO  0.1346370 0.2889291  8   0.466  0.9645
 LLO - LSF  0.7381193 0.2889291  8   2.555  0.1246
 LLO - LSO  0.2936536 0.2889291  8   1.016  0.7451
 LSF - LSO -0.4444657 0.2889291  8  -1.538  0.4605

P value adjustment: tukey method for comparing a family of 4 estimates
```

Appendix S6 Results from the post-hoc comparison of the linear mixed model for *L. polyedra* biovolume calculated for 15 days after *L. polyedra* inoculation. Relative *L. polyedra* biovolume was square root transformed. p-values were adjusted after Tukey

```
lm_ling_15<- lmer(sqrt(lingulo_bv)~ treat*pos
                 +(1|no_unit)
                 ,data=temp_data_15)
emmeans(lm_ling_15, pairwise~treat,type = "response

$emmeans
 treat response       SE df lower.CL upper.CL
 LLF    1721052 559300.7  8 672935.6  3252435
 LLO    1888355 585855.1  8 779004.3  3480973
 LSF    1209197 468810.0  8 369752.5  2531908
 LSO    1235992 473975.9  8 384635.2  2570616

Degrees-of-freedom method: satterthwaite
Confidence level used: 0.95
Intervals are back-transformed from the sqrt scale

$contrasts
 contrast   estimate       SE df t.ratio p.value
 LLF - LLO -62.28565 301.4626  8  -0.207  0.9966
 LLF - LSF 212.25380 301.4626  8   0.704  0.8927
 LLF - LSO 200.13686 301.4626  8   0.664  0.9077
 LLO - LSF 274.53945 301.4626  8   0.911  0.8001
 LLO - LSO 262.42251 301.4626  8   0.870  0.8198
 LSF - LSO -12.11694 301.4626  8  -0.040  1.0000

P value adjustment: tukey method for comparing a family of 4 estimates
```

Appendix S7 *Results from the post-hoc comparison of the linear mixed model for relative L. polyedra biovolume calculated for 15days after L. polyedra inoculation. Relative L. polyedra biovolume was square root transformed. p-values were adjusted after Tukey*

```
lm_percling_15<- lmer(sqrt(perc_lingulo)~ treat*pos
                      +(1|no_unit)
                      ,data=temp_data_15)

emmeans(lm_percling_15, pairwise~treat,type = "response")

$emmeans
 treat  response        SE df   lower.CL upper.CL
 LLF   3.3048045 1.1729469  8 1.15342478 6.563066
 LLO   3.4023275 1.1901276  8 1.21132907 6.700207
 LSF   0.9649115 0.6337956  8 0.05681698 2.979887
 LSO   1.8754184 0.8835976  8 0.39127927 4.466439

Degrees-of-freedom method: satterthwaite
Confidence level used: 0.95
Intervals are back-transformed from the sqrt scale

$contrasts
 contrast    estimate       SE df t.ratio p.value
 LLF - LLO -0.0266278 0.456237  8  -0.058  0.9999
 LLF - LSF  0.8356130 0.456237  8   1.832  0.3268
 LLF - LSO  0.4484530 0.456237  8   0.983  0.7629
 LLO - LSF  0.8622408 0.456237  8   1.890  0.3039
 LLO - LSO  0.4750808 0.456237  8   1.041  0.7316
 LSF - LSO -0.3871601 0.456237  8  -0.849  0.8303

P value adjustment: tukey method for comparing a family of 4 estimates
```

Appendix S8 Post-hoc test results (Tukey's HSD) for regional chlorophyll *a* (square root transformed) 9 days after *L. polyedra* inoculation.

```
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = chla_mean ~ treat, data = reg9_La)

$treat
             diff       lwr       upr     p adj
LLO-LLF   3.180667 -36.60618  42.96751 0.9936453
LSF-LLF 104.388667  64.60182 144.17551 0.0001416
LSO-LLF 125.219333  85.43249 165.00618 0.0000373
LSF-LLO 101.208000  61.42115 140.99485 0.0001768
LSO-LLO 122.038667  82.25182 161.82551 0.0000452
LSO-LSF  20.830667 -18.95618  60.61751 0.3936993
```

Appendix S9 *Post-hoc test results (Tukey's HSD) for regional total biovolume 9 days after L. polyedra inoculation.*

```
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = bv_mean ~ treat, data = reg9_La)

$treat
             diff       lwr       upr     p adj
LLO-LLF   5470187 -38181761  49122134 0.9766708
LSF-LLF  86400951  42749003 130052898 0.0010102
LSO-LLF 115059923  71407976 158711870 0.0001369
LSF-LLO  80930764  37278817 124582711 0.0015584
LSO-LLO 109589736  65937789 153241684 0.0001942
LSO-LSF  28658972 -14992975  72310920 0.2309450
```

Appendix S10 *Post-hoc test results (Tukey's HSD) for relative regional L. polyedra 9 days after L. polyedra inoculation.*

```
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = bv_ling_perc ~ treat, data = reg9_La)

$treat
              diff        lwr        upr     p adj
LLO-LLF  2.3126944 -0.6673557  5.2927445 0.1372092
LSF-LLF -1.3749614 -4.3550115  1.6050887 0.4917110
LSO-LLF  0.4654007 -2.5146493  3.4454508 0.9567833
LSF-LLO -3.6876558 -6.6677059 -0.7076057 0.0175080
LSO-LLO -1.8472936 -4.8273437  1.1327564 0.2691811
LSO-LSF  1.8403621 -1.1396879  4.8204122 0.2717744
```

Appendix S11 *Post-hoc test results (Tukey's HSD) for total biovolume 15 days after L. polyedra inoculation.*

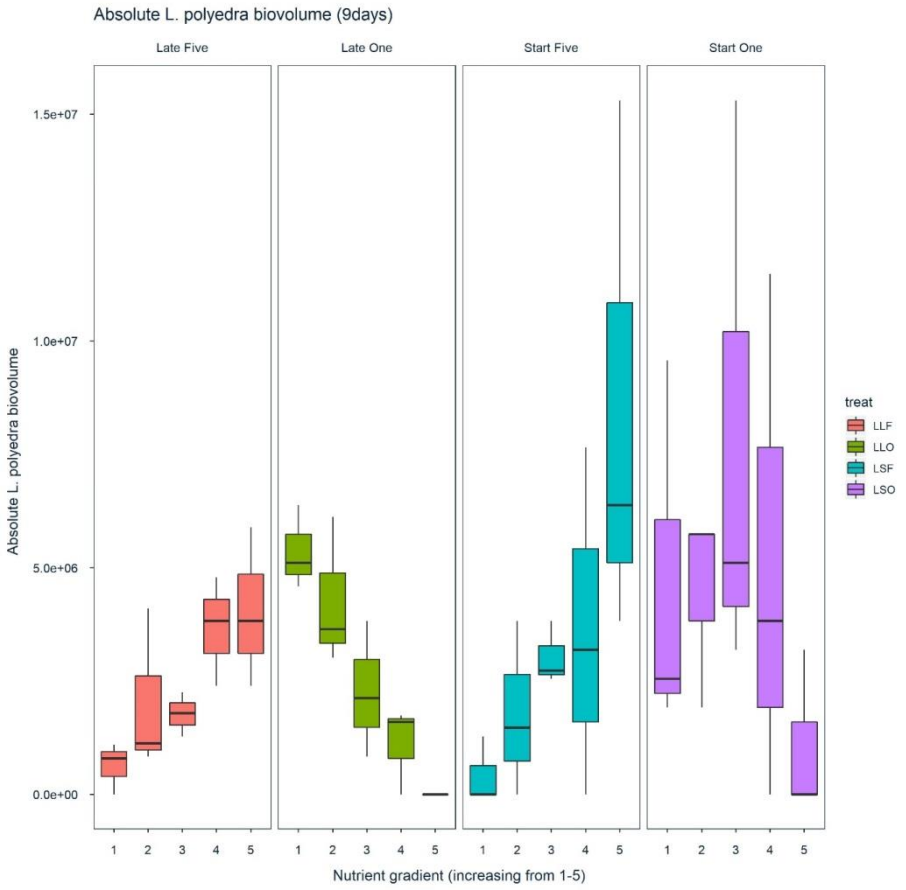
```
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = bv_mean ~ treat, data = reg15_La)

$treat
            diff         lwr      upr     p adj
LLO-LLF 15252010 -22177832.6 52681852 0.5850119
LSF-LLF 49640596  12210753.5 87070438 0.0119988
LSO-LLF 53473864  16044021.3 90903706 0.0078526
LSF-LLO 34388586  -3041256.4 71818429 0.0721787
LSO-LLO 38221854    792011.5 75651696 0.0454580
LSO-LSF  3833268 -33596574.6 41263110 0.9869208
```

Appendix S12 *Results from the post-hoc comparison of the linear mixed model for particulate C:N ratio on the last day of the experiment (day 24). C:N ratio was log transformed. p-values were adjusted after Tukey.*

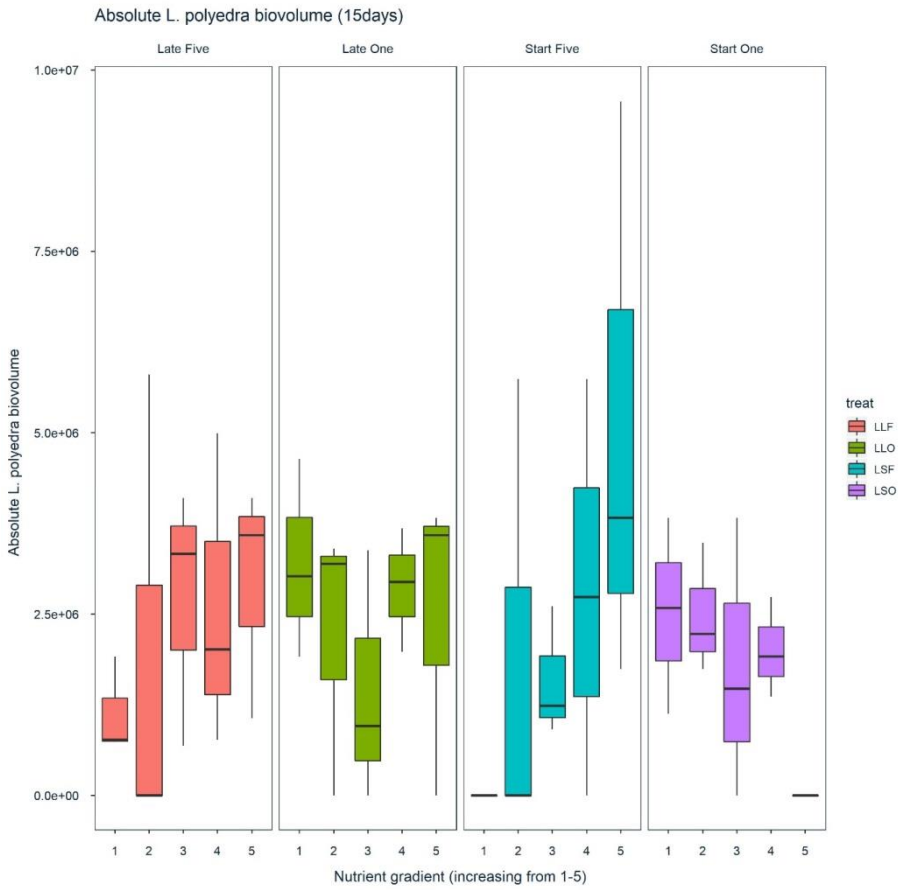
```
  lmer((log(CN_ratio))~ treat*pos
             +(1|no_unit)
             ,data=CNP_24)

emmeans(lm_cn, pairwise~treat,type = "response")

$emmeans
 treat    response         SE    df lower.CL upper.CL
 LLF      2.361962 0.03049791  9.88 2.293894 2.430031
 LLO      2.478791 0.03049791  9.88 2.410722 2.546859
 LSF      2.481148 0.03102667 10.53 2.412483 2.549813
 LSO      2.333432 0.03049791  9.88 2.265363 2.401500
 No_Lingu 2.309269 0.03049791  9.88 2.241200 2.377337

Degrees-of-freedom method: satterthwaite
Unknown transformation "(.log": no transformation done
Confidence level used: 0.95

$contrasts
 contrast           estimate         SE    df t.ratio p.value
 LLF - LLO      -0.116828709 0.04313056  9.88  -2.709  0.1230
 LLF - LSF      -0.119185840 0.04350606 10.20  -2.740  0.1153
 LLF - LSO       0.028530540 0.04313056  9.88   0.661  0.9603
 LLF - No_Lingu  0.052693326 0.04313056  9.88   1.222  0.7401
 LLO - LSF      -0.002357132 0.04350606 10.20  -0.054  1.0000
 LLO - LSO       0.145359249 0.04313056  9.88   3.370  0.0448
 LLO - No_Lingu  0.169522034 0.04313056  9.88   3.930  0.0190
 LSF - LSO       0.147716380 0.04350606 10.20   3.395  0.0416
 LSF - No_Lingu  0.171879166 0.04350606 10.20   3.951  0.0175
 LSO - No_Lingu  0.024162786 0.04313056  9.88   0.560  0.9780

P value adjustment: tukey method for comparing a family of 5 estimates
```

Appendix S13 *Post-hoc test results (Tukey's HSD) for regional C:N ratio on the last day of the experiment (day 24).*

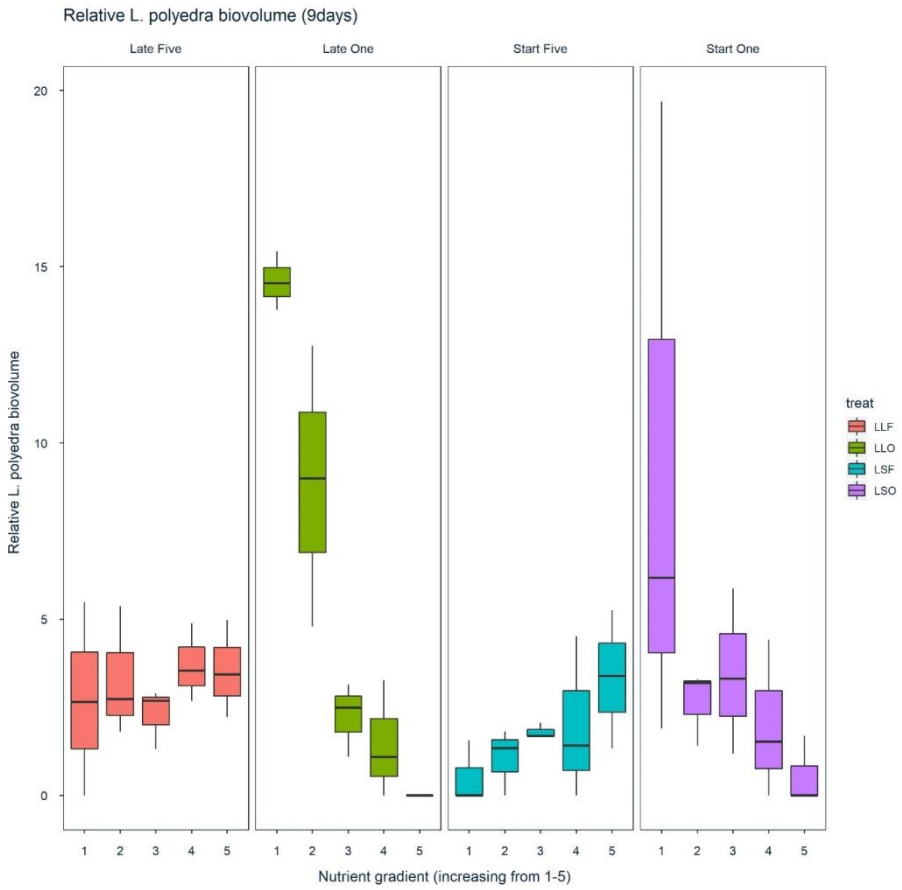
```
    Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = cn_mean ~ treat, data = regional_cnp)

$treat
                    diff        lwr         upr     p adj
LLO-LLF       1.37386934 -0.3156727  3.06341141 0.1282710
LSF-LLF       1.46182185 -0.2277202  3.15136392 0.0990401
LSO-LLF      -0.30117685 -1.9907189  1.38836522 0.9740782
No_Lingu-LLF -0.55921849 -2.2487606  1.13032358 0.8081958
LSF-LLO       0.08795251 -1.6015896  1.77749458 0.9997702
LSO-LLO      -1.67504618 -3.3645883  0.01449589 0.0522397
No_Lingu-LLO -1.93308783 -3.6226299 -0.24354576 0.0239603
LSO-LSF      -1.76299870 -3.4525408 -0.07345663 0.0400372
No_Lingu-LSF -2.02104034 -3.7105824 -0.33149828 0.0184079
No_Lingu-LSO -0.25804165 -1.9475837  1.43150042 0.9852237
```



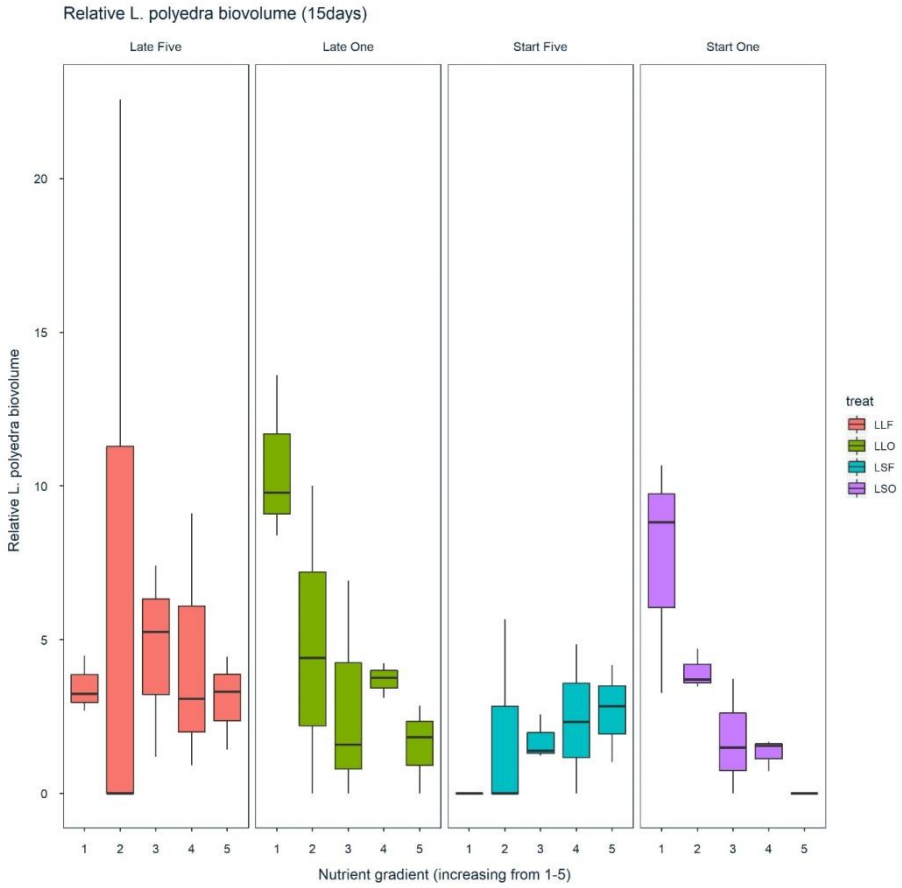
Appendix S14 *Mean L. polyedra biovolume ($\mu m^3 ml^{-1}$) ± SD over the nutrient gradient, only for 9 days after the L. polyedra inoculation. $Start_{one}$ $Start_{five}$ reperesent results from nine days after the start of the experiment, wheres $Late_{one}$ and $Late_{five}$ represent results from 18 days after the start of the experiment.*



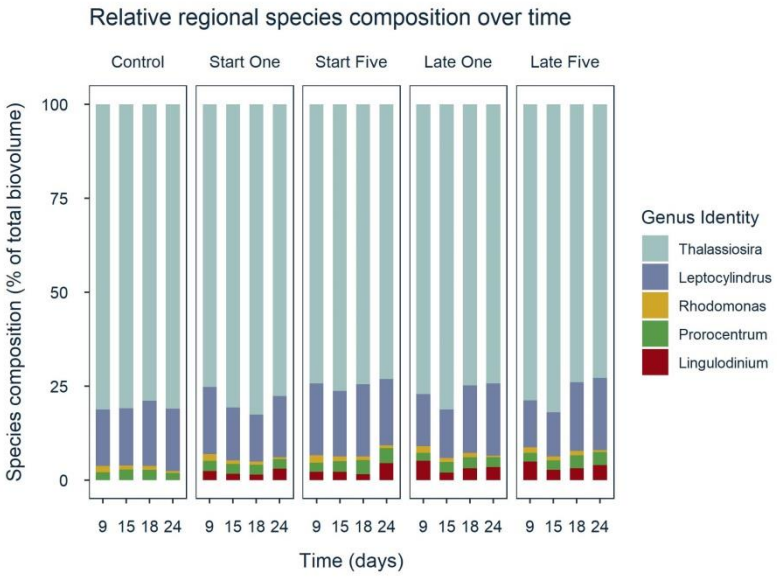
Appendix S15 *Mean L. polyedra biovolume ($\mu m^3 ml^{-1}$) ± SD over the nutrient gradient, only for 15 days after the L. polyedra inoculation. $Start_{one}$ $Start_{five}$ reperesent results from 15 days after the start of the experiment, wheres $Late_{one}$ and $Late_{five}$ represent results from the end of the experiment (after 24 days).*



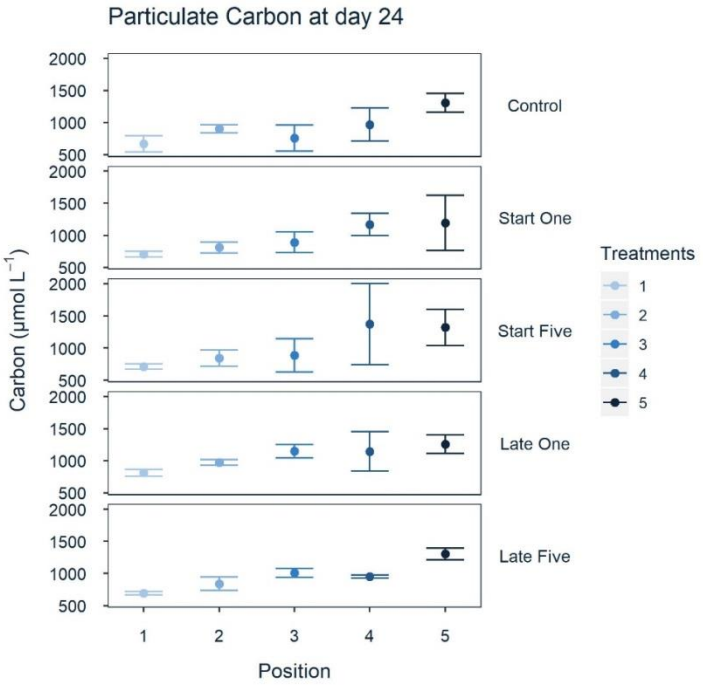
Appendix S16 *Mean relative L. polyedra biovolume ± SD over the nutrient gradient, only for 9 days after the L. polyedra inoculation. $Start_{one}$ $Start_{five}$ reperesent results from nine days after the start of the experiment, wheres $Late_{one}$ and $Late_{five}$ represent results from 18 days after the start of the experiment.*



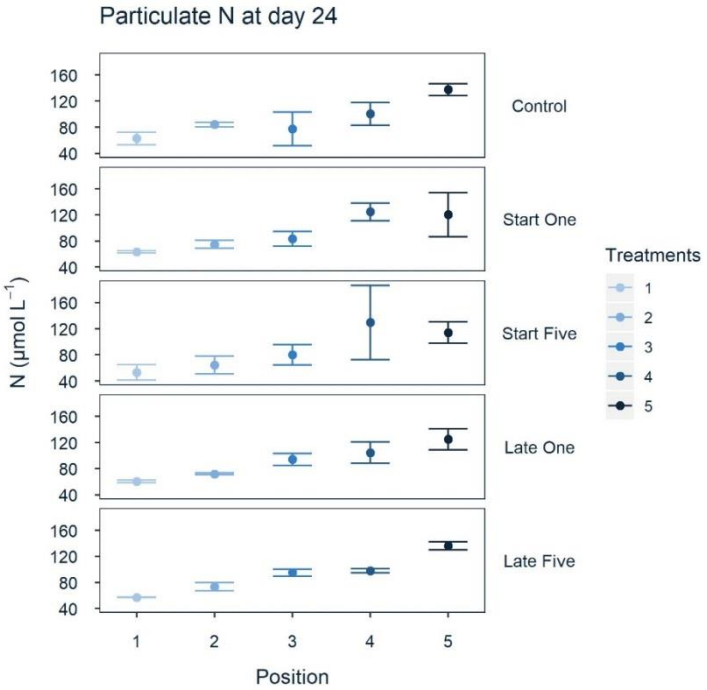
Appendix S17 *Mean relative L. polyedra biovolume ± SD over the nutrient gradient, only for 15 days after the L. polyedra inoculation. $Start_{one}$ $Start_{five}$ reperesent results from 15 days after the start of the experiment, wheres $Late_{one}$ and $Late_{five}$ represent results from the end of the experiment (after 24 days).*



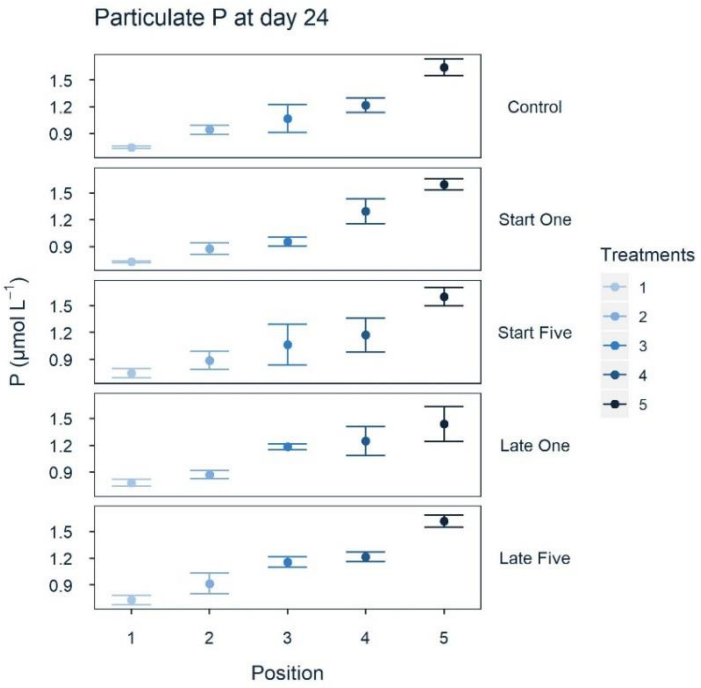
Appendix S18 *Relative regional species composition (% of the total phytoplankton biovolume), shown as stacked bar charts over time. Regional biovolume was calculated by the mean of all five flasks of one meta-ecosystem. Plot was split up into inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$).*



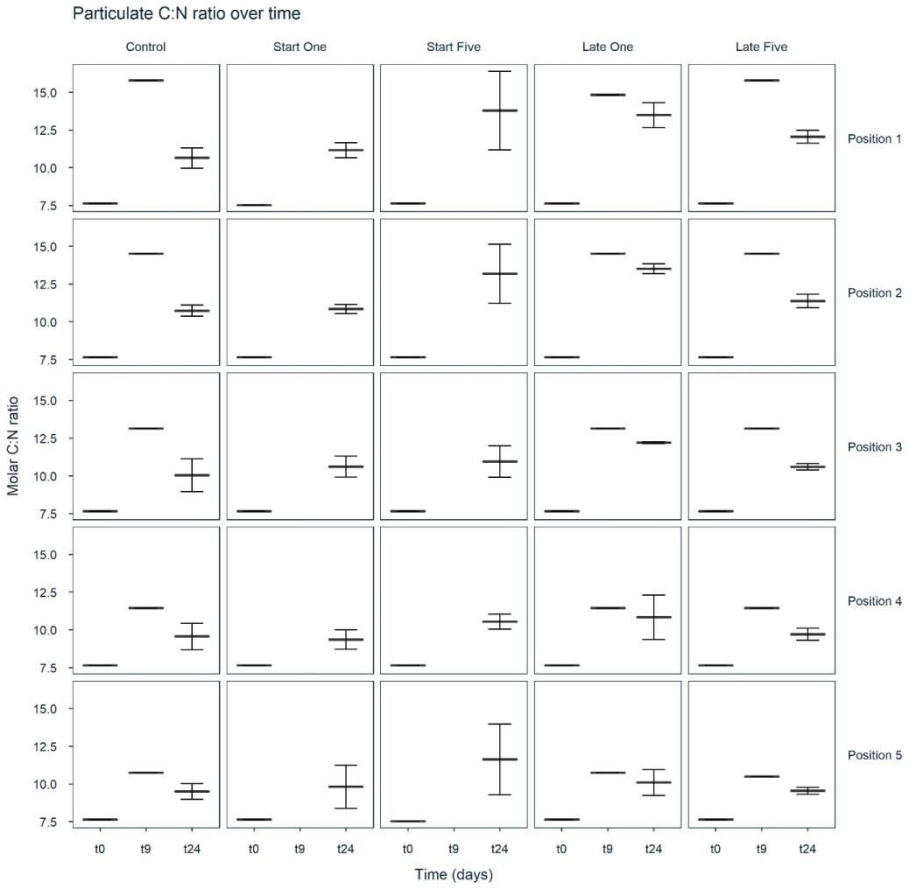
Appendix S19 *Mean particulate carbon ± SD (µmol L^{-1}) at the last day of the experiment (day 24) over increasing nutrient concentration (position along the nutrient gradient). Plots are split up into inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$). Colors indicate the in the respective position from light (position 1) to dark blue (position 5).*



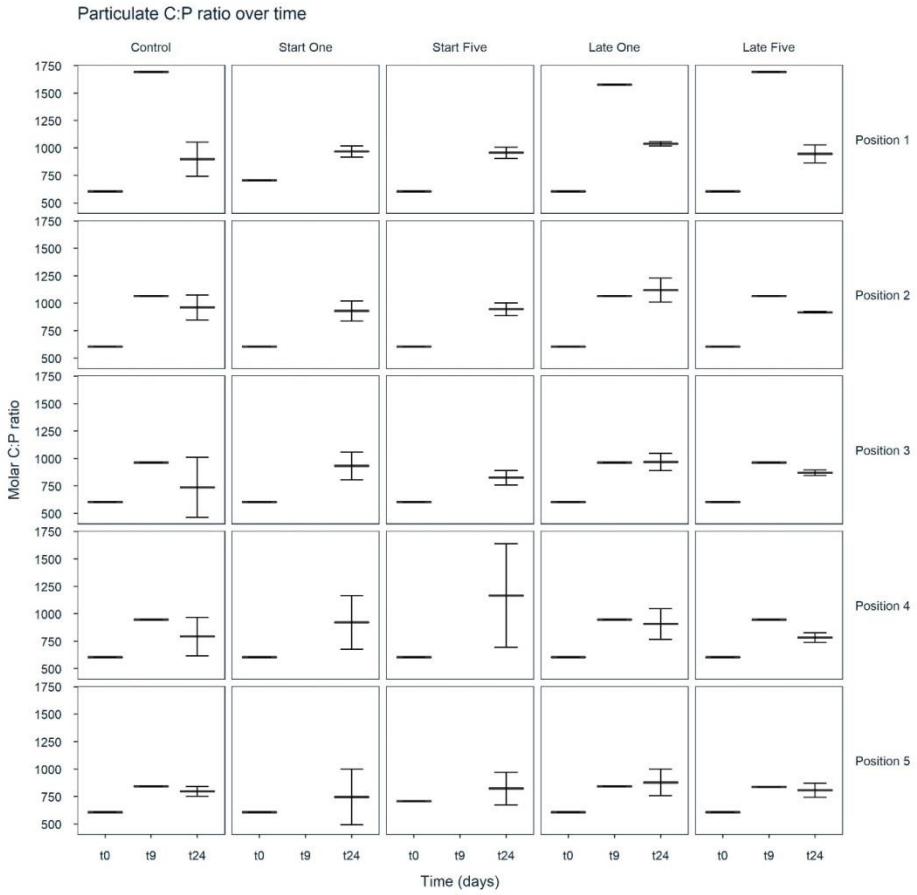
Appendix S20 *Mean particulate nitrogen ± SD (µmol L^{-1}) at the last day of the experiment (day 24) over increasing nutrient concentration (position along the nutrient gradient). Plots are split up into inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$). Colors indicate the in the respective position from light (position 1) to dark blue (position 5).*



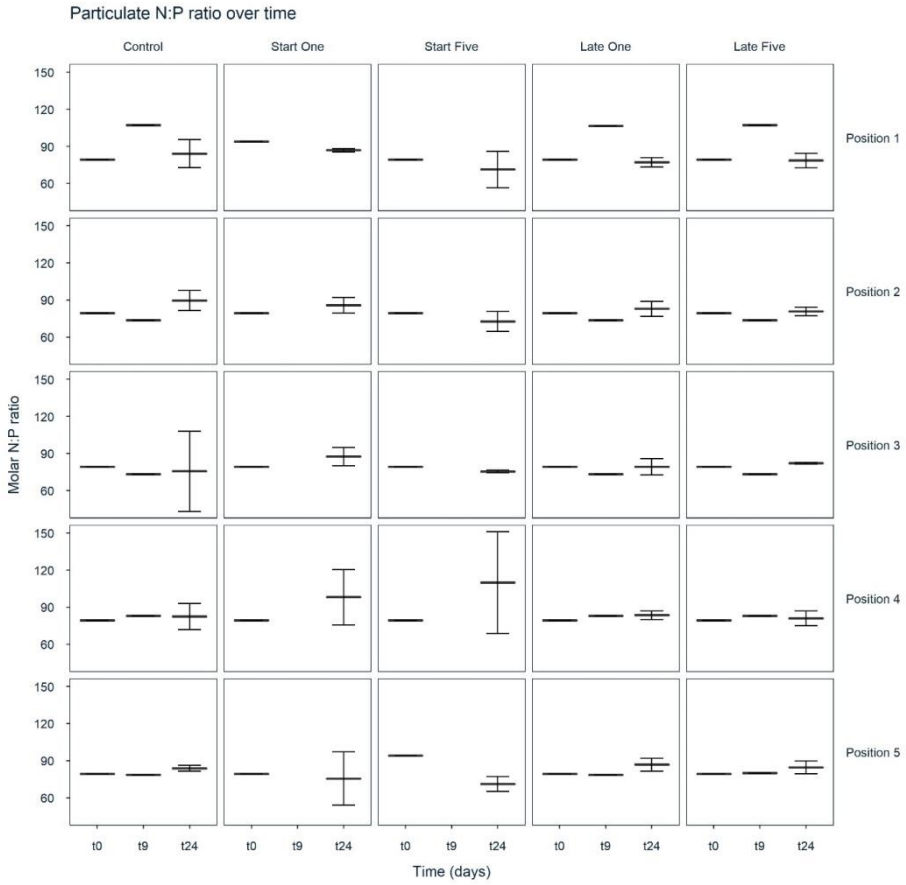
Appendix S21 *Mean particulate phosphorous ± SD (µmol L^{-1}) at the last day of the experiment (day 24) over increasing nutrient concentration (position along the nutrient gradient). Plots are split up into inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$). Colors indicate the in the respective position from light (position 1) to dark blue (position 5).*



Appendix S22 *Mean molar particulate C:N ratios ± SD at day 0, 9 and 24. Plots are split up into inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$) and along the position of the nutrient gradient.*



Appendix S23 *Mean molar particulate C:P ratios ± SD at day 0, 9 and 24. Plots are split up into inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$) and along the position of the nutrient gradient.*



Appendix S24 *Mean molar particulate N:P ratios ± SD at day 0, 9 and 24. Plots are split up into inoculation treatments (Control, $Start_{one}$, $Start_{five}$, $Late_{one}$, $Late_{five}$) and along the position of the nutrient gradient.*

Chapter 3

The blooming enigma of *Lingulodinium polyedra*: Influences of the timing of nutrient pulses on dinoflagellate dominated communities

Abstract

In upwelling regions like the Southern Californian Coast, a variety of factors can influence phytoplankton bloom dynamics. The red tide dinoflagellate *Lingulodinium polyedra* is often abundant in this region during summer and autumn. *L. polyedra* can form dense blooms, which can, after the decay, lead to rapid oxygen depletion. As *L. polyedra* bloom patterns are still not completely understood, it remains unclear which factors drive bloom formation and persistence of this species.

Here, I investigated bloom persistence and population dynamics during an autumn bloom of the dinoflagellate *L. polyedra* along the southern Californian coast. I studied L. polyedra bloom dynamics in relation with community structure and the timing of nutrient additions. Two experiments with natural phytoplankton communities from the blooms edge were conducted. In order to investigate nutrient pulse effects, dissolved nutrients were either added at the beginning or after a 'starvation' phase, mimicking natural nutrient variability, such as in upwelling regions. In addition, nutrient pulses were added with and without silicate addition, to analyse diatom and dinoflagellate interactions.

Overall, neither nutrient composition of the pulse, nor timing promoted bloom persistence or formation of *L. polyedra*. Even with an initial biomass contribution of more than 70%, *L. polyedra* decreased quickly. However, overall phytoplankton biomass increased in all treatments with the input of nutrients. Phytoplankton composition thus rapidly changed from a dinoflagellate dominated into a diatom-dominated community. My results showed that initial community structure was important for the responses to the nutrient pulse, as it influenced biomass and dissimilarity differently.

While the *L. polyedra* bloom vanished in my experiment, it was reported to persist in the field for a longer period. My results suggest that nutrient pulses, at least as a single factor, are not the drivers for *L. polyedra* bloom persistence. As potential grazers increased with decreasing dinoflagellate abundance, it is likely, that initial filtering had promoted grazing, as it excluded higher trophic levels and thus predators of these grazers. In addition, it is possible, that nutrient input is only beneficial for this bloom-forming dinoflagellate in combination with other factors, such as spatial migration or light.

Introduction

Harmful algal blooms (HABs) and their versatile negative effects have raised public health concerns and have caused huge economic losses for decades (Dyson and Huppert, 2010; Gibble et al., 2016; Horner et al., 1997). Bloom dynamics of HABs in upwelling areas are complex and not fully understood, as they appear to be the result of a variety of environmental factors. Compared to the winter-spring diatom bloom, which is usually predictable and persistent, the classical upwelling diatom blooms emerge as a series of recurring blooms, which are separated by upwelling-relaxation periods in which often dinoflagellates bloom (Smayda and Trainer, 2010). Different studies have reported that dinoflagellates have a great storage capacity for inorganic and organic nutrients (Collos et al., 2004; Dagenais-Bellefeuille and Morse, 2013; Maguer et al., 2007), increasing their competitive success under low nutrient conditions in highly dynamic systems, such as upwelling areas, where nutrients fluctuate. In upwelling areas, the potential of dinoflagellates to form a bloom is therefore influenced by the duration, intensity and ratio between upwelling and relaxation periods,

resulting in strong nutrient driven competitive interactions between diatoms and dinoflagellates (Margalef, 1978).

The Eastern Boundary Upwelling Ecosystems (EBUEs) represent some of the world's most productive marine ecosystems, where the four biggest EBUEs (Canary, California, Humboldt and Benguela) provide one fifth of the global marine fish catch (Fréon et al., 2009). Similar to the other big EBUES, the California current system can be partitioned into subdivisions; northern, central and southern California (Checkley and Barth, 2009; Fréon et al., 2009). The coast of Southern California, belonging to the Californian EBUE, is therefore one of the 'hot-spots' for different algal blooms, including a huge variety of harmful algae (Horner et al., 1997; Kudela et al., 2010; Trainer et al., 2010). The California Current System and the Southern Californian region, in particular, has been shown to exhibit a lower primary production, compared to other upwelling regions, like the Peru Current, or the Southern Benguela, which is related to offshore Ekman transports (Ware, 1992). Yet, Kahru *et al.* (2009) showed in a time series from 1997 to 2007 that the net primary production has significantly increased in this region, but reasons for this increase were unclear.

Bloom development in upwelling systems is also influenced by hydrodynamics, as HABs can propagate through the transport via ocean currents (Franks and Kaefer, 2003). For instance, Bialonski et al. (2016) provided evidence for the importance of hydrodynamic transport for the occurrence and propagation of HABs by studying the connectivity of different areas in the Southern Californian Bight. However, stimulation and potential bloom development of harmful algal species were not only dependent on current patterns, but also on local environmental conditions, such as nutrient concentrations. Aside from abiotic factors, local conditions also include biotic interactions, such as competition between species and grazing, which can play an important role for bloom formation, persistence and termination (Admiraal and Venekamp, 1986; Calbet and Landry, 2004; Strom, 2001; Strom and Morello, 1998; Zhai et al., 2013).

Along the coast of Southern California, harmful algal blooms caused by dinoflagellates are a common phenomenon, which potentially have severe impacts on the ecosystem due to the production of toxins or due to oxygen depletion (Horner et al., 1997; Kudela and Cochlan, 2000; McGowan et al., 2018). The red tide dinoflagellate *Lingulodinium polyedra* (F. Stein) J. D. Dodge 1989 (formerly *Gonyaulax polyedra*; by many authors *Lingulodinium polyedrum*), which is often abundant in this region during summer and autumn, is a high-density bloomer,

reaching bloom densities of more than 2 x 10^7 cells L^{-1} (Allen, 1946; Bruno et al., 1990; Hayward et al., 1995; Holmes et al., 1967; Kahru and Mitchell, 1998; Marasovic, 1989). Thus its blooms can lead to oxygen depletion due to microbial degradation of high biomass blooms, which may kill fish or invertebrates (Horner et al., 1997; Kudela and Cochlan, 2000). Along the Southern Californian Coast, *L. polyedra* blooms occur rather regularly (e.g. Kudela and Cochlan, 2000; McGowan et al., 2018; Moorthi et al., 2006). However, they do not follow a strict blooming pattern.

Many HAB species have evolved a variety of species-specific strategies increasing their competitive strength and/or decreasing grazing pressure, such as mixotrophic feeding, where cells obtain energy both via photosynthesis and particle ingestion, which can be a competitive advantage over strict photo- and heterotrophs (Bockstahler and Coats, 1993; Burkholder et al., 2008). This feeding strategy has also been found for *L. polyedra,* especially under nutrient depleted conditions (Busch, 2016). Some dinoflagellates, like *Alexandrium tamarense*, produce allelochemicals as secondary metabolites with a lytic activity that can decrease the survival, growth and/or reproduction of other, potentially competing, species (Rice, 1983; Tillmann and Hansen, 2009). *L. polyedra*, however, has not been found to produce allelopathic substances (Busch, 2016), yet, it has been shown to produce yessotoxin. Yessotoxin is a hepato- and cardiotoxin, which, to date, has not been demonstrated to have toxic effects on humans (Armstrong and Kudela, 2006; Munday, 2014; Paz et al., 2004), but it has been shown to be toxic for mice when injected intraperitoneal (Aune et al., 2002; Tubaro et al., 2003). In the Southern California Bight, no adverse effects on marine mammal associated with yessotoxin have been reported so far (Caron et al., 2010).

Blooms of *L. polyedra* are associated with warm weather conditions (Allen, 1946; Eppley and Harrison, 1975; Holmes et al., 1967) and mainly occur after the coastal upwelling season under stratified conditions (Horner et al., 1997), when a shallow (< 10m) nutrient depleted mixed surface layer has formed above a steep thermocline separating it from deep, nutrient-rich water (Eppley and Harrison, 1975). However, nutrient conditions in upwelling systems fluctuate, and *L. polyedra* has also been found in large numbers in nutrient-rich surface layers, which had developed due to a high nutrient freshwater runoff after heavy rainfalls (Hayward et al., 1995).

In two previously conducted laboratory experiments (see Chapter 1&2), I tested the effect of a nutrient gradient on the spatial dynamics of two bloom-forming dinoflagellates (*Alexandrium catenella* in Chapter 1 and *Lingulodinium polyedra* in Chapter 2) in simple phytoplankton communities consisting of five species assembled from laboratory cultures. My results showed that both studied dinoflagellate species were better competitors under low nutrient concentrations, especially at a late successional phase of the community. In both experiments, diatoms formed a bloom at the beginning, which was then followed by a stronger impact of dinoflagellates after the demise of the diatom bloom. Similar patterns were found in field studies e.g. of Georges Bank (Gettings et al., 2014) or the Bornholm Basin (van Beusekom et al., 2009). The results of my previous conducted experiments indicated that nutrient input and phytoplankton community composition, or rather, the successional state of a community are important determinants for bloom dynamics of harmful dinoflagellates (Chapter 1, Chapter 2). Therefore, as part of the second experiment (Chapter 2), I investigated the effect of the inoculation timing of *L. polyedra* into the assembled community at different successional states. Both inoculation timings of *L. polyedra* (early and late), had only weak effects on the *L. polyedra* bloom development itself. Thus, it raised the question whether the timing of the nutrient pulse depending on the successional state of the community might be more relevant in natural communities, as nutrient input through rivers or via upwelling is not a constant influx but rather occur as pulses.

Studies aiming to explain bloom formation of *L. polyedra* have mainly focused on the physiology and ecology of this species in monocultures or its interaction with few selected species, but rarely within highly complex natural communities (e.g. Jeong et al., 2005; Paz et al., 2004; Stauffer et al., 2017). Laboratory studies with artificially assembled, simple communities provide a good method to study specific trophic interactions and processes and help to gain a more mechanistic understanding. However, in complex, natural communities, patterns might be different due to other interacting factors, such as the presence of multiple trophic levels and therefore higher grazing pressure and competition. It is therefore important to also study trophic interactions of the target species in complex natural communities.

In this study, I, therefore, investigated population dynamics and competitive interactions of the red tide dinoflagellate *L. polyedra* during an autumn bloom at the Southern Californian Coast. I focused on the influence of initial plankton community composition and the timing of

nutrient pulses mimicking the natural nutrient variability occurring in upwelling regions. I conducted two experiments with natural phytoplankton communities taken from two different locations at different dates of the *L. polyedra* bloom. Initial communities of both locations differed in their species composition and biomass since different environmental biotic and abiotic factors shape local ecosystems, their community composition and biomass distribution. I followed *L. polyedra* bloom dynamics in dependency of the plankton community structure and the timing of nutrient pulses at different successional states of the communities. Therefore, dissolved nutrients were either added as a pulse at the beginning of each experiment or after a 'starvation' phase of three days into each community. Dissolved nutrients were either added as dissolved nitrogen (N) and phosphorus (P) only or as N, P and silicate (Si). These two different nutrient compositions were tested in order to get a better understanding of competitive interactions of dinoflagellates and diatoms.

With this experiment I tested the following hypotheses:

H1: A nutrient pulse, independent of the timing and composition (NP or NPSi) increases phytoplankton biomass.

H2: Nutrient composition affects *L. polyedra* dominance and overall community composition. A nutrient pulse including silicate (NPSi) particularly promotes diatoms, while a nutrient pulse without Si promotes other species including *L. polyedra*.

H3: The timing of the nutrient pulse affects *L. polyedra* dominance and overall community composition, depending on the initial community composition.

H3.1: An early nutrient pulse will be beneficial for already dominating phytoplankton species, while a late pulse will promote species that compete better under low nutrient conditions.

H3.2: If *L. polyedra* initially dominates the community, either nutrient pulse will promote it; if the community is dominated by other species, *L. polyedra* will be only promoted by a late nutrient pulse due to its ability to store nutrients (nitrogen).

Methods

Experimental set-up

I conducted two laboratory experiments using different plankton communities collected from two different sites and dates off the coast of Los Angeles (California, USA). Samples were collected during a *Lingulodinium polyedra* bloom to study the effect of the timing and the composition of a nutrient pulse on the dominance of *Lingulodinium polyedra* and overall community dynamics. Both experiments were conducted following the same protocol and are therefore described together. Initial plankton samples were collected on the edge of the *L. polyedra* bloom, to start the experiment with a high *L. polyedra* dominance, but at the same time include potential competitor species. As the bloom persisted over several weeks in the same region, both locations were close to each other within the Los Angeles County, California, USA. The location Zuma Beach (Lat.:34° 2' 2.4'' N; Long.: 118° 51' 14.4'' W) was sampled on the 15th September 2017, whereas Point Dume (Lat.: 34° 0' 46.8'' N; Long.: 118° 49' 15.6'' W) was sampled on the 09th October 2017 (Fig. 1B). At both locations, surface water was collected from a few meters off the shore. Water was immediately filtered through a 200 µm gauze to exclude mesozooplankton > 200 µm such as copepods and filled into carboys. Carboys were fully filled to avoid air bubbles in the water during the transportation into the laboratory, which could have destroyed, for instance, fragile microzooplankton such as ciliates.

The experiments were carried out in 1L bottles, which were air-bubble free filled with the seawater of the respective location. In each experiment, I set up four different nutrient treatments. The treatments received a single nutrient pulse consisting of either nitrogen and phosphorus (NP) or N, P and silicate (NPSi). These different nutrient compositions were either added at the beginning of the experiment ("NP_{early}", "$NPSi_{early}$") or after a "starvation" phase of three days ("NP_{late}", "$NPSi_{late}$").

The added amount of nutrients resulted in a final concentration of 13.44 µmol/l nitrogen, 0.84 µmol/l phosphorous and, if included, 12.60 µmol/l silicate. These concentrations approximate the Redfield-Brzezinski ratio (Brzezinski, 1985) and were equal to the lowest nutrient concentration in the previously conducted experiments (Chapter 1 & 2). In addition, I set up a control treatment, where no nutrients were added. All treatments and the control were

replicated four times, resulting in a 2x2x4 factorial treatment design, and a total of 20 flasks per experiment (location). All flasks were randomly placed into a temperature constant (17.5 °C) incubator with a 12:12 (day: night) light rhythm with a light intensity of 100 µmol m^{-2} s^{-1}.

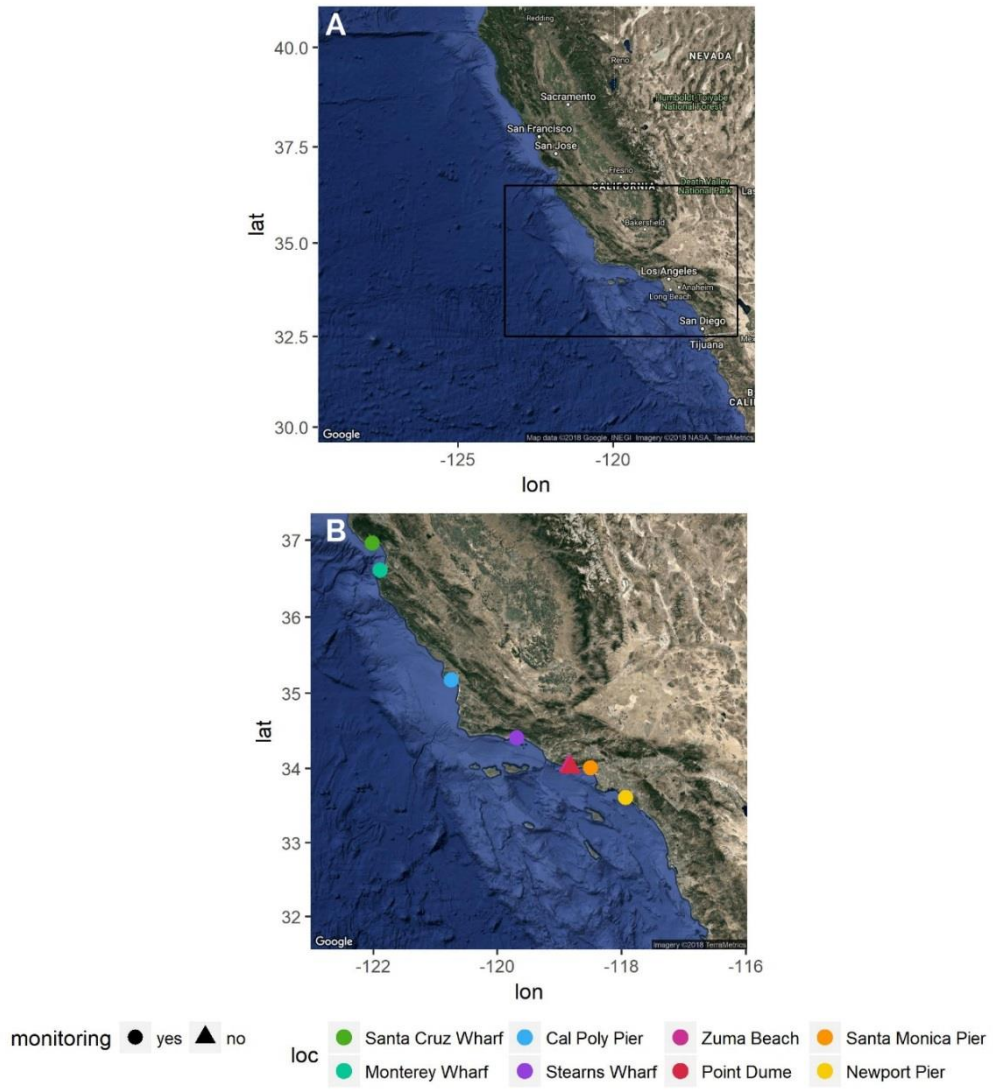


Figure 1 A: Overview of the Southern Californian Bight. Black box marks the sampling are of the SCCOOS HAB-Monitoring stations, which have been included in the HAB-Monitoring between August and December 2017 B: Sampling sites of this experiment were marked as triangles, sampling sites within the SCCOOS HAB-Monitoring are represented by circles

Both experiments ran for 15 days. All flasks were sampled every third day (t3, t6, t9, t12, t15). At each sampling day, flasks were gently shaken for homogenization, and a total volume of 134ml was removed. For microscopic community analyses, 50 ml subsamples were fixed with 1% Lugol's iodine and stored at 4°C in dark coloured bottles until further analyses. For in situ measurements, I used 4ml for in-vivo chlorophyll absorption measurements (Turner Designs,

Inc. Sunnyvale, Ca, USA) as a proxy for biomass development. For the determination of extracted chlorophyll *a* concentration, 80ml subsamples from each bottle were filtered on GF/F Whatman filters and extracted in 100% acetone for 24h at -20°C in the dark and analysed by fluorometry (Turner Designs, Inc. Sunnyvale, Ca, USA).

Community analyses

Fixed samples were settled in Utermöhl sedimentation chambers for 24h. Depending on the measured absorption and extracted chlorophyll *a*, a volume of 15 – 25 ml was used for sedimentation. Samples were counted at different magnifications under an inverted light microscope (Leica DM IRB). Since this study focused on the bloom development of *L. polyedra*, all *L. polyedra* cells were counted in the entire settled sample at a magnification of 10x. After assuring that all cells were homogenously distributed within the sample, ten grids at a magnification of 50x were counted to ensure, that rare but big species were included in the composition analyses. However, *Phaeocystis* sp. and *Noctiluca* sp. have been excluded from the analyses, for which only very few cells (*Noctiluca* sp. in only two samples) or colonies (*Phaeocystis* sp. in only one sample) were counted, but through their huge, disproportionate size, and the calculation steps, their total biovolume was extremely overrated. A total of 50 grids at a magnification of 400x was counted for all phytoplankton species, as well as microzooplankton, such as ciliates and rotifers. Most samples contained a large number of small unidentifiable flagellates, which were, due to their large amount, only counted in 10-20 of the 50 grids and categorised into two size classes (<10µm and <3µm in diameter). All counted grids were randomly chosen.

All phytoplankton species were classified into five taxonomic groups: Diatoms, Dinoflagellates, Chlorophytes, Cryptophytes and Others (consisting of small unidentifiable flagellates, and *Dictyocha* sp. and *Chattonella* sp.). All counted cells were identified to species level, if possible. Cell numbers of phytoplankton were used to calculate the respective biovolume of each species. However, it was not possible to measure the size of all species alive in order to calculate the biovolume. In addition, the fixation with Lugol's iodine was shown to potentially alter the cell size (Menden-Deuer et al., 2001). Therefore, the respective individual species/genus biovolume was derived from databases (Appendix Table 1; *Nordic Microalgae*

and aquatic protozoa; *Encyclopedia of Life and literature therein*) Biovolume was used, in addition to the chlorophyll *a* values, as a proxy for algal biomass. If individual species or genus biovolume had multiple size classes, the mean was used for the calculations. All cells which could not be identified to genus level were excluded from the analyses, as their biovolume could not be calculated (unidentifiable cells represented between 0.1 – 3.2% of all cells and between 0.3 – 10.3% of all cells, when small flagellates were excluded, as they represent high cell numbers but low biomass). Small, unidentifiable flagellates were included, for which biovolume was calculated as a spherical shape for the determined size classes. As phytoplankton could not all be identified on the species level, community analyses were conducted on genus level.

Despite the initial filtering, mesozooplankton >200 µm was found in the samples of both experiments, which was therefore counted in the same way as phytoplankton. However, zooplankton (including micro- and mesozooplankton) was only assessed as cells and not considered in any biovolume calculations, e.g. the total biovolume. After the first sampling of the second experiment (location Point Dume), an overall higher amount of copepods was noticed. Therefore, I scanned the entire flask three times on each sampling day, in order to count all living copepods (adults and nauplii) and extrapolated copepod cell numbers per litre.

Calculations and statistical analyses

All statistical analyses and graphs were performed using R version 3.4.3 (R Core Team, 2016) and the following packages: vegan, ggplot2, lme4, lsmeans, lmerTest, grid.

Diversity was calculated based on genus level, including the two different size groups of small unidentifiable flagellates. Diversity was assessed as the effective number of species (ENS), which is a true diversity measure, and calculated as the inverse Simpson index (Jost, 2006). ENS describes the number of hypothetical equally abundant species which are needed to obtain the same mean proportional species abundance as the actual species did (Tuomisto, 2010). Thus ENS equals the actual number of species (species richness) only if all species are equally abundant (Tuomisto, 2010). For this analysis, ENS was calculated with the genus biovolume. Thus ENS represented the effective number of genera. However, for consistency of the method, I will proceed with the abbreviation ENS.

In addition, differences in species composition were assessed with the Bray Curtis dissimilarity (Bray and Curtis, 1957). Both, ENS and the Bray-Curtis dissimilarity were calculated using the vegan package. The log response ratio (LRR) was calculated as the natural log-transformed ratio of total biovolume in a nutrient treatment over the mean total biovolume in the control, to test the effect of the different nutrient treatments on total algal biovolume, (Hedges et al., 1999).

The effect of the nutrient treatments on total algal biovolume, *L. polyedra* biovolume, relative *L. polyedra* biovolume, total biovolume, extracted chlorophyll *a*, ENS, LRR and Bray-Curtis dissimilarity were tested using linear mixed models. These models included the treatment (nutrient composition and timing of the nutrient pulse) and time as fixed factors as well as the individual flask ID and time as random factors. I used the lmerTest package to compare the fixed factors and the interaction with a type 3 ANOVA with Satterthwaite's method. Both experiments (locations) were analysed separately.

Results

Initial conditions

Both communities had a similar initial phytoplankton biomass (Fig. 2,3), as well as a similar composition of taxonomic groups, with a clear dominance of dinoflagellates (Fig. 4). However, initial samples strongly differed in their species composition. Especially my focus organism *L. polyedra* had a much stronger dominance at Point Dume, representing more than 70% of the total biomass (30111 cells L^{-1}), compared to Zuma Beach, where it represented only around 20% (7350 cells L^{-1}, Fig 5,7). In addition to *L. polyedra, Prorocentrum* sp. represented almost 20% and *Gymnodinium* around 5% of the community biomass of Point Dume, emphasising the very strong initial dinoflagellate dominance at this location. At Zuma Beach, *Gymnodinium* sp. was the main component in determining dinoflagellate dominance with more than 50% of the total biovolume. In contrast to Point Dume, other groups, like diatoms were present in higher biovolume, such as *Hemialus* sp. which represented around 6% of the total biovolume.

At both locations, micro- and mesozooplankton was found. Zuma Beach exhibited a higher initial amount of 3746 individuals L^{-1} (Fig. 12), consisting of a mixture of the ciliate *Mesodinium*

sp. and tintinnids, whereas the initial community of Point Dume only consisted of *Mesodinium sp.* (Fig. 13). Overall, both locations represented two different communities where dominance structures were distributed differently.

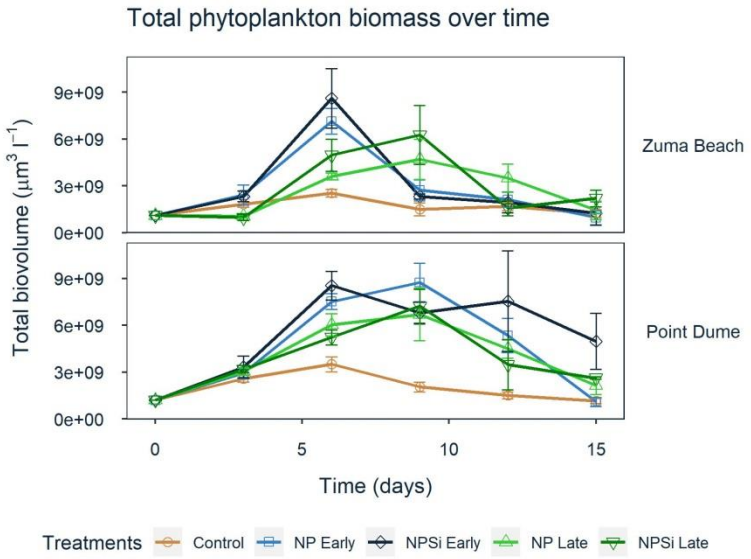


Figure 2 *Mean total biomass (µm³ L⁻¹) ± SE over time split up into the two different locations, Zuma Beach and Point Dume as well as into the different nutrient pulse treatments*

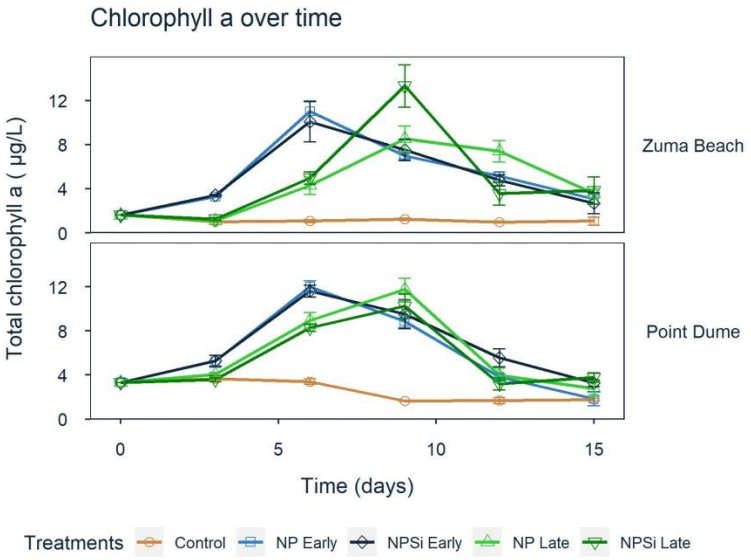


Figure 3 *Mean total chlorophyll a (µg L⁻¹) ± SE over time split up into the two different locations, Zuma Beach and Point Dume as well as into the different nutrient pulse treatments*

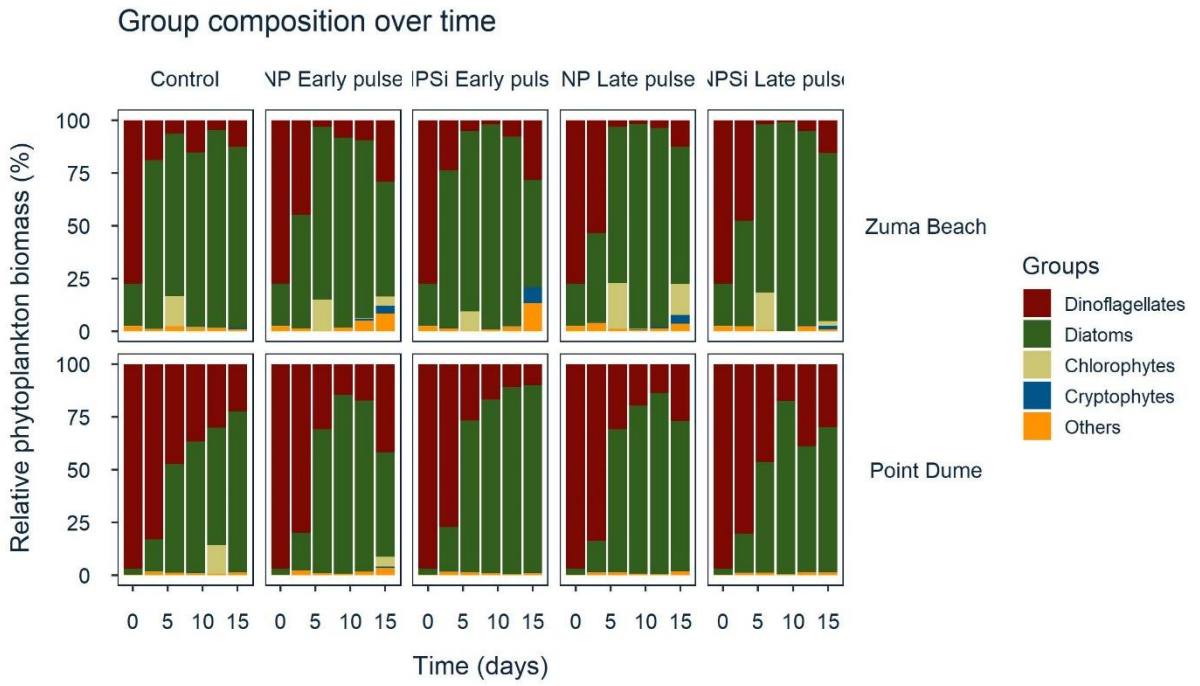


Figure 4 Group composition over time, split up into the two different location, as well as into the different nutrient pulses

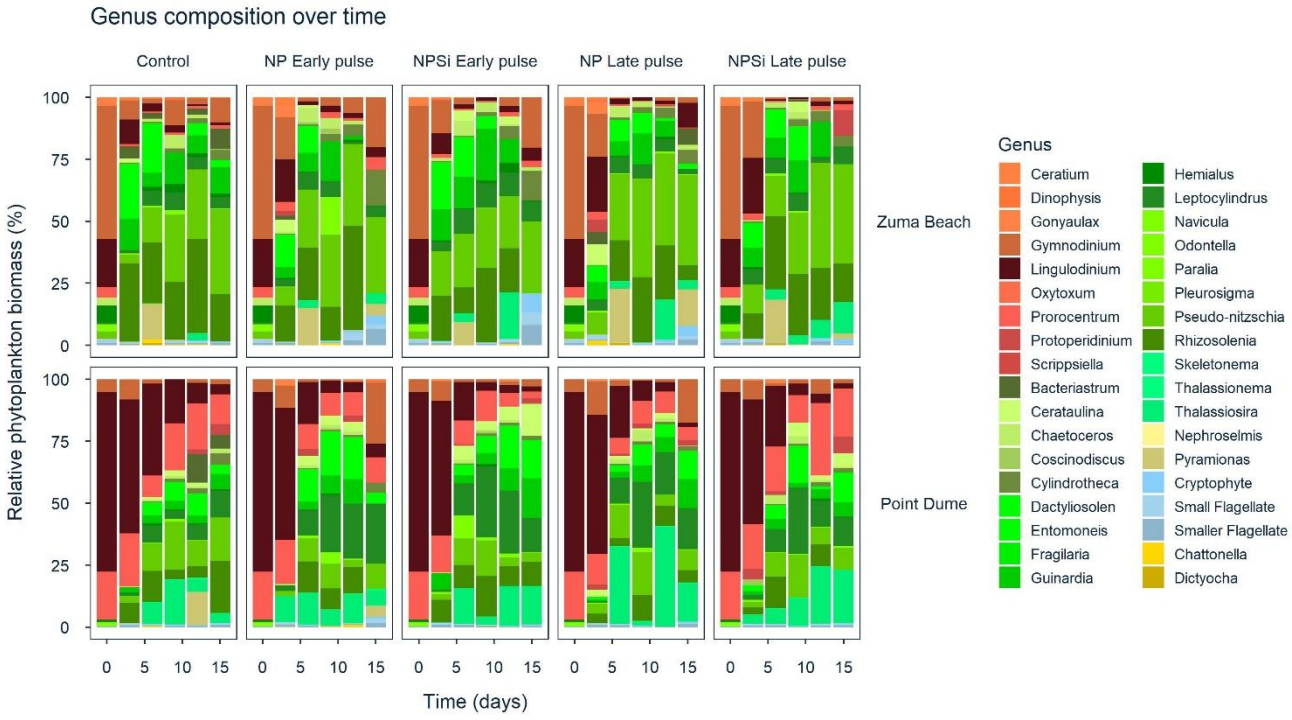


Figure 5 Genus composition over time, split up into the two different location, as well as into the different nutrient pulses

Phytoplankton biomass dynamics

Biomass was measured as extracted chlorophyll *a*, as well as by the calculated biovolume, based on the microscopic counts. While both measures showed the same trends (Fig. 2,3), only chlorophyll *a* measurements showed significant effects of the different treatments, where the control exhibited significantly lower biomass than all other treatments ($p<0.05$, Tab. 1). Overall, total biomass increased in all treatments of both locations in the first few days, after which it decreased. The temporal development of algal biomass depended on the timing of the nutrient pulse, with earlier peaks in treatments with an early nutrient pulse and later peaks in the treatments of the later nutrient pulse (Fig. 2, 3). I can, therefore, accept the first hypothesis (H1), stating that a nutrient pulse increases biomass.

Early pulses resulted in an early biomass peak after six days, while late pulses led to a later and weaker peak, after nine days, which was, equal to the early addition, six days after nutrient addition. However, also the total algal biomass in the control increased within the first days, but to a lower magnitude compared to the nutrient treatments. The initial biomass increase was followed by a mostly steady decrease, which was stronger in treatments exposed to the late nutrient pulse. At the end of the experiment, all treatments reached a similar biomass level. A steeper biomass increase was observed, followed by a stronger decrease in both nutrient composition treatments for the communities of Zuma Beach getting the early nutrient pulse (Fig. 2). This was, however, not represented in the chlorophyll *a* data (Fig. 3). Phytoplankton biovolume was higher in the nutrient addition treatments compared to the control, but this was only significant for the community of Point Dume for both early pulses (with and without Si addition, $p>0.05$, Tab. 1B).

Table 1 *Community responses of the linear mixed models; A: Chlorophyll a, B: Phytoplankton biomass, C: Log Response Ration (LRR), D: Effective number of species (ENS), E: Bray-Curtis Dissimilarity*

	Response		Zuma Beach			Point Dume		
A	Chlorophyll *a*	Factor	df	F	p	df	F	p
		Treatment	4	2.872	*<0.05*	4	3.568	*<0.01*
		Time	1	0.467	0.532	1	0.060	0.819
		Treatment : Time	4	2.217	0.072	4	1.141	0.341
			Zuma Beach (log transformed)			Point Dume		
B	Total phytoplankton biomass	Factor	df	F	p	df	F	p
		Treatment	4	1.845	0.125	4	0.518	0.723
		Time	1	0.010	0.952	1	0.276	0.627
		Treatment : Time	4	2.844	*<0.05*	4	2.445	*<0.05*
			Zuma Beach			Point Dume		
C	LRR	Factor	df	F	p	df	F	p
		Treatment	4	1.973	0.104	4	0.647	0.632
		Time	1	0.003	0.959	1	2.731	0.173
		Treatment : Time	4	3.053	*<0.05*	4	4.772	*<0.01*
			Zuma Beach			Point Dume		
D	ENS	Factor	df	F	p	df	F	p
		Treatment	4	0.655	0.624	4	0.314	0.868
		Time	1	0.215	0.667	1	3.212	0.148
		Treatment : Time	4	1.495	0.210	4	1.006	0.409
			Zuma Beach			Point Dume		
E	Bray-Curtis Dissimilarity	Factor	df	F	p	df	F	p
		Treatment	4	2.126	0.085	4	1.280	0.283
		Time	1	7.444	0.053	1	36.260	*<0.01*
		Treatment : Time	4	3.147	*<0.05*	4	6.517	*<0.001*

Log response ratio (LRR)

I used the log response ratio (LRR) of the total biomass (calculated with biovolume) as a proxy for net changes between the treatments and the control (Fig. 6) over time, which varied between the timing of the nutrient pulse and the locations. However, no statistically significant differences could be found between different nutrient treatments (Tab. 1C). Yet, the LRR was significantly higher than zero for all nutrient treatments of Point Dume only ($p>0.05$, Tab. 1C), showing, that biomass was overall higher than the control.

The influence of the nutrient addition led to a positive response ratio of LRR>0 in all nutrient treatments at both locations. One of the major differences between both locations was that the LRRs remained positive for the community of Point Dume in all treatments (Fig. 6), except for the NP_{early} treatment at day 15, whereas the LRRs of Zuma Beach decreased below zero towards the end of the experiment.

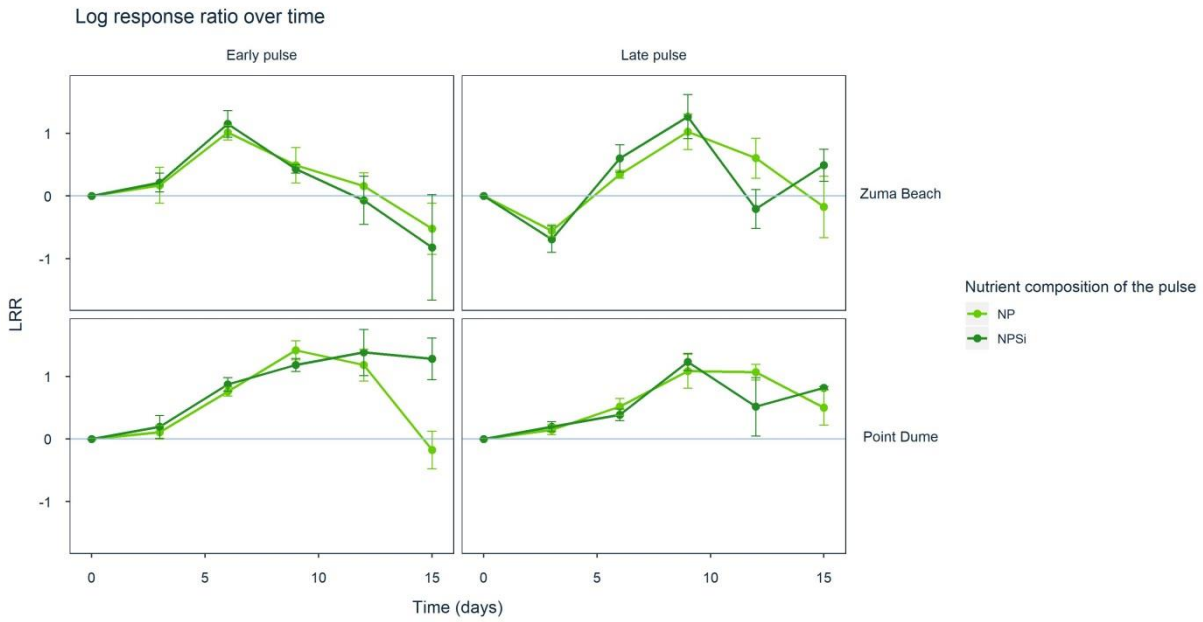


Figure 6 *Mean log response ratio (LRR) ± SEof the total phytoplankton biovolume over time, split up into the two different location, as well as into the different nutrient pulses; blue line represents the control. If values are above this line, they have a higher biomass, than the control.*

For the community of Zuma Beach, the early pulse of nutrients led to an LRR increase until day 6, which was followed by a linear decrease, which even reached negative LRRs at the end of the experiment (Fig. 6). The LRR of the community of Point Dume, in contrast, increased over a longer period. The early addition of NPSi was followed by logistic growth, with a saturation of the LRR around 1. In this case, the positive effect of the nutrient addition lasted until the end of the experiment, whereas the NP_{early} addition had its peak at day 9 and decreased thereafter with a strong decline and an LRR < 0 at the end of the experiment. At day 15, there was a strong discrepancy between the LRRs of the NP and NPSi addition in the communities of Point Dume.

In the treatments subject to a late nutrient pulse, the community of Zuma Beach experienced an initial LRR drop at day 3 (Fig. 6). At this time, treatments should have been similar to the control, since nutrients were added after that sampling. Apart from this early decrease, the late addition of nutrients led to an increase in the LRR until day 9 in both locations. While the LRR of the NP_{late} treatment of Point Dume remained stable for the following days and

decreased thereafter, the LRR of the NP_{late} treatment of Zuma Beach decreased steadily from day 9 on and even reached a negative value at the end of the experiment. The $NPSi_{late}$ treatments of both locations also increased until day 9, after which they strongly decreased (Fig. 6). Only at Zuma Beach, this decrease reached a negative LRR on day 12. In both communities, LRRs increased again at the end of the experiment.

L. polyedra dynamics

Despite differences in *L. polyedra* absolute and relative biomass development between both locations, within each location, biomass development was highly similar, with only minor treatment differences (Fig. 7, 8). Therefore, no significant differences in absolute or relative *L. polyedra* biomass between treatments and controls for neither of both locations were found over the course of the experiment (Tab. 2A & B).

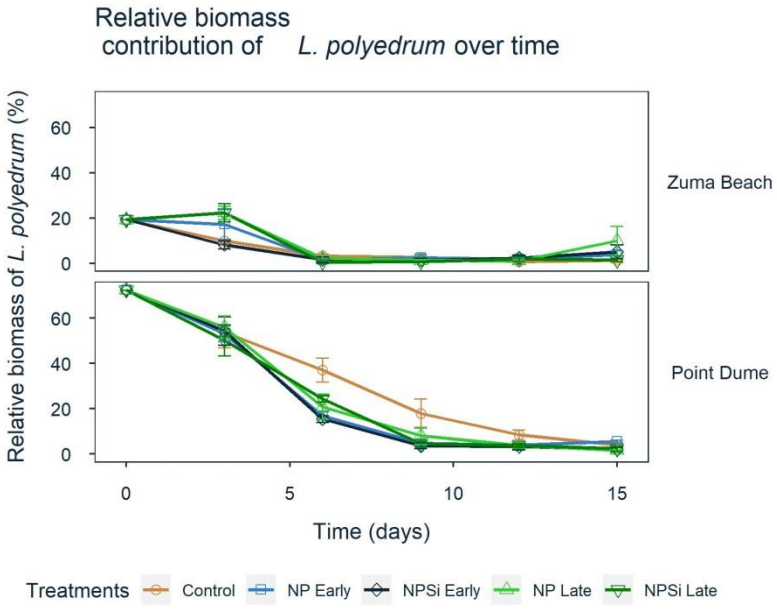


Figure 7 *A: Mean Relative biomass(%) ± SE of L. polyedra over time; Both results are split up into the two different location, as well as into the different nutrient pulses*

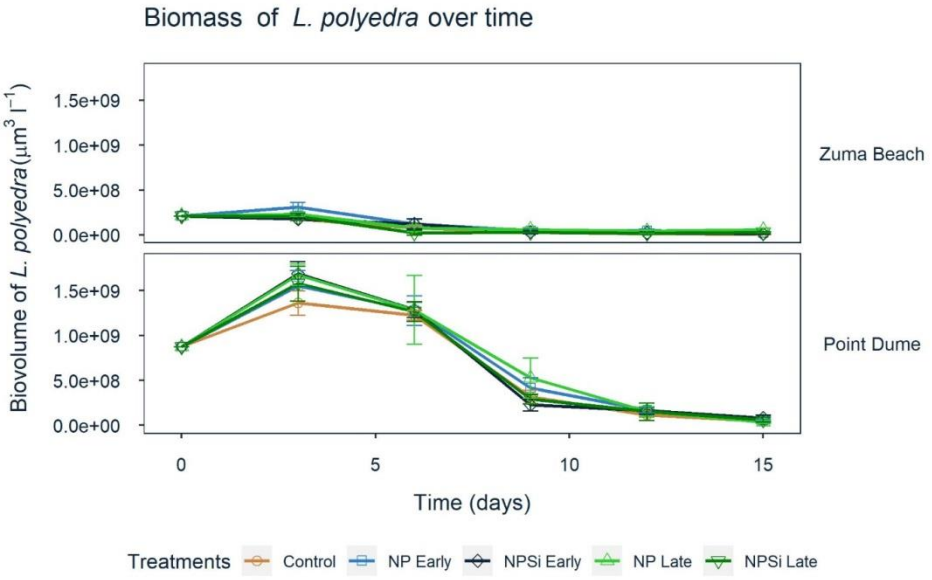


Figure 8 *Mean total biomass (µm³ L⁻¹) ± SE of L. polyedra; Results are split up into the two different location, as well as into the different nutrient pulses*

Table 2 *L. polyedra relative and absolute biomass responses of the linear mixed models; A: biomass, B: Relative proportion as percentage of the total phytoplankton biomass*

	Response		Zuma Beach			Point Dume		
		Factor	df	F	p	df	F	p
A	*L. polyedra* biomass	Treatment	4	2.000	0.102	4	0.381	0.821
		Time	1	19.450	*<0.05*	1	6.815	0.059
		Treatment : Time	4	0.670	0.613	4	0.174	0.952

			Zuma Beach (log+1 transformed)			Point Dume		
		Factor	df	F	p	df	F	p
B	Relative proportion of *L. polyedra*	Treatment	4	0.512	0.727	4	0.970	0.431
		Time	1	6.045	0.0698	1	27.246	*<0.01*
		Treatment : Time	4	1.156	0.336	4	0.231	0.920

Initial *L. polyedra* concentrations at Zuma Beach were low (7350cells L^{-1}). However, they still represented almost 20 % of the community biomass at the beginning of the experiment (Fig. 7,8). *L. polyedra* maintained its biomass for the first three days, which was then followed by a decrease. From day 6 on, *L. polyedra* represented less than 4% of the total biomass in this community, irrespective of the nutrient treatment. Relative proportions, as well as absolute concentrations of L. polyedra, remained low until day 12 (0.9 - 2.4% and 508 – 1650 cells L^{-1} at day 12). At day 15, relative proportions in the $NPSi_{early}$ treatment increased up to 5% and up to 10% in the NP_{late} treatment (Fig. 7), whereas absolute biomass remained low.

In contrast, at Point Dume, starting concentrations of *L. polyedra* were high (30111 cells L^{-1}), representing more than 70% of the total biomass (Fig. 7, 8). Overall, *L. polyedra* absolute and relative biomass decreased drastically over the course of the experiment (Fig. 7, 8), with the exception of the first three days, where *L. polyedra* absolute biomass even increased. However, this increase was present in all treatments and the control, showing, that it was independent of the different nutrient additions. From day nine on, relative contributions were below 5%, except for the control. While the control exhibited a lower absolute *L. polyedra* biomass within the first six days, it had a higher relative biomass from day six to day 12.

Overall, the nutrient composition of the pulse had no effect on the absolute nor on the relative biomass of *L. polyedra*. Thus, I have to reject my second hypothesis (H2), that a pulse without Si would promote *L. polyedra*. As I also did not find any *L. polyedra* bloom promotion due to the timing of the nutrient pulse, I have to reject H3.2, stating that a nutrient pulse, independent of the timing, will promote a bloom, if initial dominance of *L. polyedra* is high (such as initial conditions at Point Dume) and that lower initial *L. polyedra* abundance (such as in Zuma Beach), would only be promoted by a late nutrient pulse.

Phytoplankton group and genus dynamics

Initial dinoflagellate contributions to total algal biomass decreased at both locations and dinoflagellates were replaced mostly by diatoms, irrespective of the type of nutrient pulse (Fig. 4). This decrease of dinoflagellates was more drastic for the communities of Zuma Beach and more gradual for the communities of Point Dume. Overall, dinoflagellates and diatoms

were the most prominent taxa, other groups, such as small flagellates had only a minor influence on the total biomass.

Dinoflagellates contributed high amounts to the total biomass in the community of Zuma Beach (Fig. 4), which was mostly represented by *Gymnodinium* sp. (53.8%) and *L. polyedra* (19.3%). However, both species decreased quickly (Fig. 5, 7, Appendix Fig. 1), leading to the overall decrease in dinoflagellates over time (Fig. 4). A variety of diatoms increased their abundances, such as *Dactyliosolen* sp., *Rhizosolenia* sp., and *Pseudonitzschia* sp. (Fig. 5). From day 6 or day 9 on, depending on the treatment, relative dinoflagellate concentrations slightly increased again in all treatments, and the control (Fig. 4). In the community from Point Dume, dinoflagellates dominated at the beginning of the experiment, mostly due to high amounts of *L. polyedra* (Fig. 4, 5, 7), but dinoflagellates quickly decreased and were mostly replaced by different diatom species (Fig. 4). The more prominent ones were *Dactyliosolen* sp*., Leptocylindrus* sp*.,* and *Thalassiosira* sp. (Fig. 5). Dinoflagellates of the genus *Prorocentrum* were present throughout the entire experiment with up to 29% of the total biomass. Despite the constant decrease in total dinoflagellate biovolume, relative dinoflagellate contributions increased again at the end of the experiment in the NP_{early} treatment as well as both late nutrient pulse treatments (NP_{late}, $NPSi_{late,}$ Fig, 4).

Communities from both locations exhibited a similar community development for all treatments and the control, showing the transition from a dinoflagellate dominated community to a diatom-dominated community (Fig. 4). Since I did not find strong differences of the species/genus composition between communities subject to different timings or compositions of nutrient pulses, I can reject H3.1, that the timing of nutrient pulses will shape the community composition by promoting either the already dominant species, or species which are better competitors under low nutrient conditions

The transition from a dinoflagellate-dominated towards a diatom-dominated community was not promoted by the silicate addition since similar patterns were visible in the control and in treatments without silicate addition. This also supports the rejection of H2, which states that diatoms will generally be favoured if silicate is added to the nutrient pulse.

ENS

The community structure was analyzed by calculating the effective number of species (ENS) based on the genera biovolume contribution. In both communities, the ENS was low at the beginning of the experiment (3 at Zuma Beach, below 2 at Point Dume, Fig. 9), as species richness was much higher (15 at Zuma Beach, 12 at Point Dume, data not shown). Especially the community of Point Dume was highly dominated by only *L. polyedra* at the start of the experiment (Fig. 5, 7), leading to this low initial ENS value. However, the ENS increased within the first days of both experiments in all treatments, including the control. While the ENS of Zuma Beach decreased again after 6 days and fluctuated around the initial value, the ENS of Point Dume fluctuated around a higher value of about 4.8 from day 6 on (Fig. 9). Despite the differences between both locations, I found no significant differences between the ENS of the nutrient additions within each community (Tab. 1D).

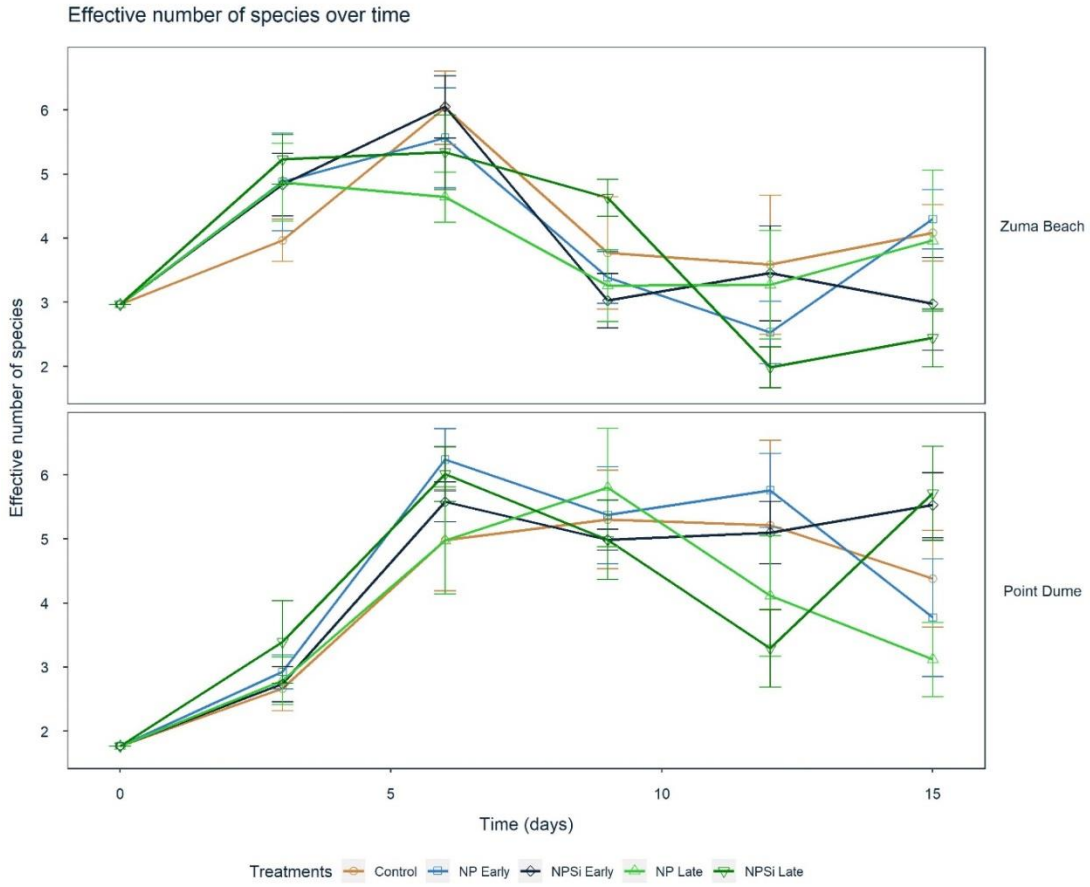


Figure 9 *Effective number of species ± SE over time; Both results are split up into the two different location, as well as into the different nutrient pulses*

Relating algal biomass to Bray-Curtis dissimilarity

I analyzed the Bray Curtis dissimilarity between the control community and the communities of the different nutrient treatments in order to access community changes in response to the nutrient input. Dissimilarity to the control strongly increased in communities from both locations at the beginning of the experiment, especially in the first three days, after which this increase decelerated and eventually saturated (Fig. 10). However, the community of Zuma Beach reached a dissimilarity maximum already after three days, after which it fluctuated around this value. Dissimilarity in different nutrient treatments increased over time, emphasizing the pronounced interaction between the nutrient treatments and time ($p=0.05253$, Tab. 1E). The dissimilarity for the community of Point Dume, in contrast, increased almost linearly for 9 days and reached a plateau at day 12. This increase was also significant over time ($p<0.01$, Tab. 1E) as well as the interaction of the treatments with time ($p<0.001$, Tab. 1E).

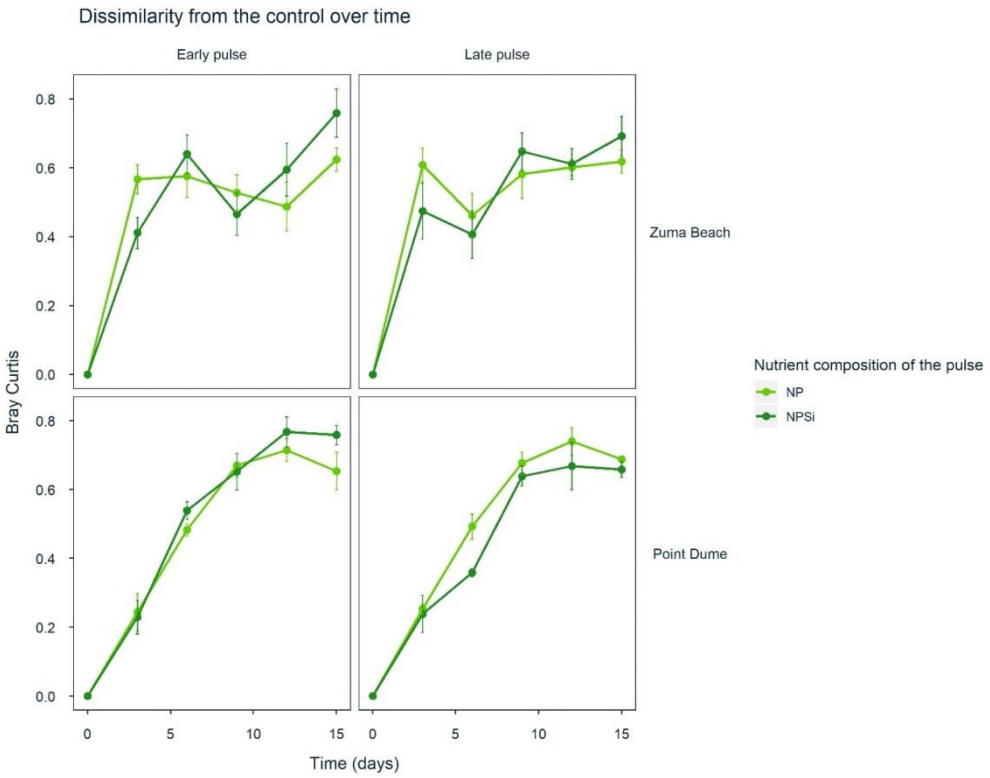


Figure 10 *Mean log response ratio (LRR) ± SE of the total phytoplankton biovolume over time, split up into the two different location, as well as into the different nutrient pulses; blue line represents the control. If values are above this line, they have a higher biomass, than the control.*

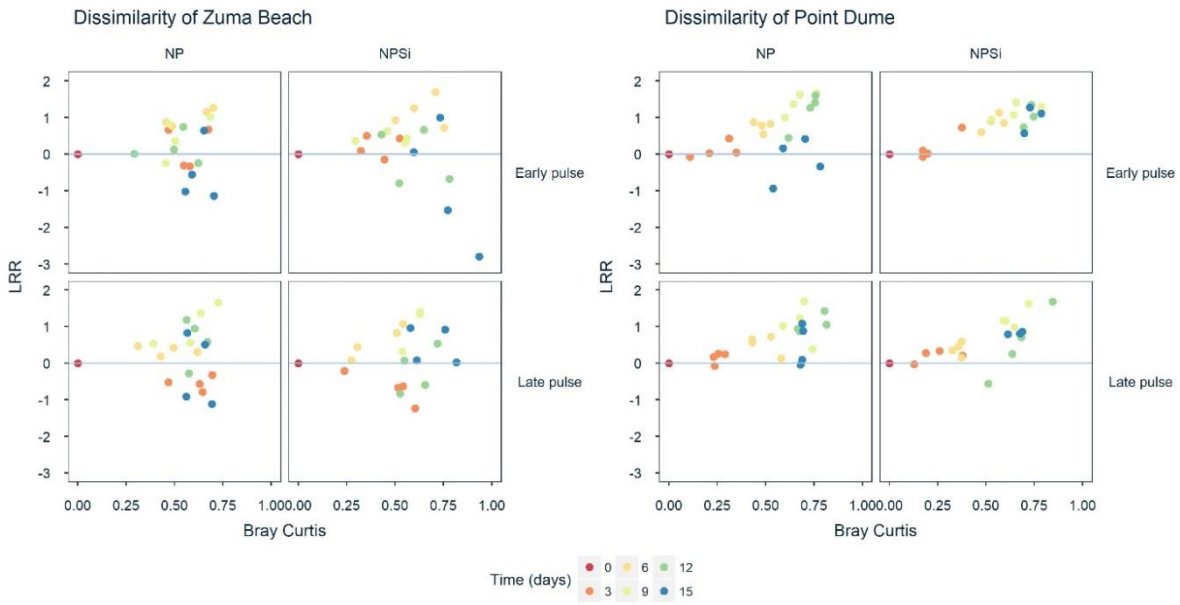


Figure 11 *LRR of the total biomass in comparison to the control over Bray-Curtis dissimilarity representing the dissimilarity of the community from the control-community, split up into the two different location, as well as into the different nutrient pulses. Colors represent the different time points*

Comparing the LRR of the total biomass with dissimilarity over time (Fig. 11) allow me to investigate temporal patterns of the community development in more depth. The community of Point Dume exhibited a clear temporal direction of the community development in relation to the control (Fig. 11). In all treatments, the LRR increase was accompanied by an increase in dissimilarity among different communities. After nine to twelve days, not only logistic growth stopped and even decreased in treatments without silicate, but also dissimilarity reached its stable state. Both, LRR and dissimilarity reflect a distinct temporal succession of the community of Point Dume. In contrast, LRR and the dissimilarity of the community of Zuma Beach showed less distinct patterns (Fig. 11). LRR, as well as dissimilarity, varied much stronger, and, as mentioned before, LRRs even reached negative responses. Overall, variation between replicates increased, and no differences between the different pulse timings, or between the nutrient compositions of the pulse were found. The community of Zuma Beach did neither show a clear pattern nor a strong connection between LRR and dissimilarity.

Zooplankton Dynamics

Ciliate concentrations were relatively low (mean of all treatments and all time points 3405 L^{-1}) and stable in the communities of Zuma Beach irrespective of the nutrient treatment

(p=0.9908, Tab. 3A), whereas concentrations strongly increased in the communities of Point Dume (Fig. 12), however without significant differences among different treatments (Tab. 3A). In the community of Point Dume, ciliate numbers followed total algal biomass, as they strongly increased at the beginning and decreased towards the end of the experiment (Fig. 12). This increase also appeared in the control, but there it reached a plateau at day 6 and decreased after day 9. Overall, ciliate abundances were higher in all nutrient treatments compared to the control. Maximum ciliate abundances were similar among different nutrient treatments, but the timing of the peaks varied. Ciliate numbers of the NP_{early} treatment increased the fastest and reached the highest numbers already on day 6. When also silicate was added ($NPSi_{early}$), the increase of ciliates was slower, but lasted until day 12, after which it decreased. The late addition of nutrients followed a similar increase in ciliate abundance until day 9, after which ciliates still slightly increased in the NP_{late} treatment but decreased in the $NPSi_{late}$ treatment.

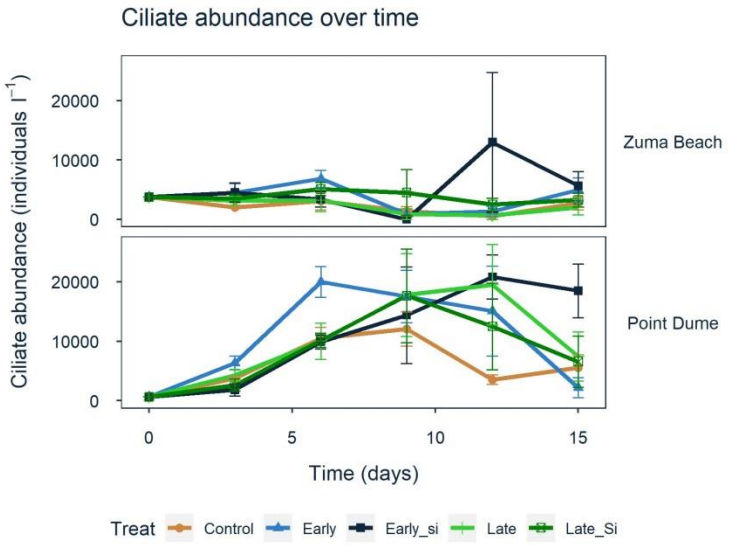


Figure 12 *Mean ciliate abundance (individuals per Litre) ± SE over time, split up into the two different location, as well as into the different nutrient pulses*

At both locations, ciliate composition changed from a *Mesodinium* sp. dominated community towards a mixture of tintinnids and unidentified oligotrich ciliate taxa. Overall, the community of Zuma Beach exhibited a higher amount of tintinnids in the beginning. Towards the end of the experiment, the community was highly dominated by unidentified oligotrichs. The

community of Point Dume, in contrast, developed into a relatively even mixture of *Mesodinium* sp. and unidentified oligotrichs (Fig. 13).

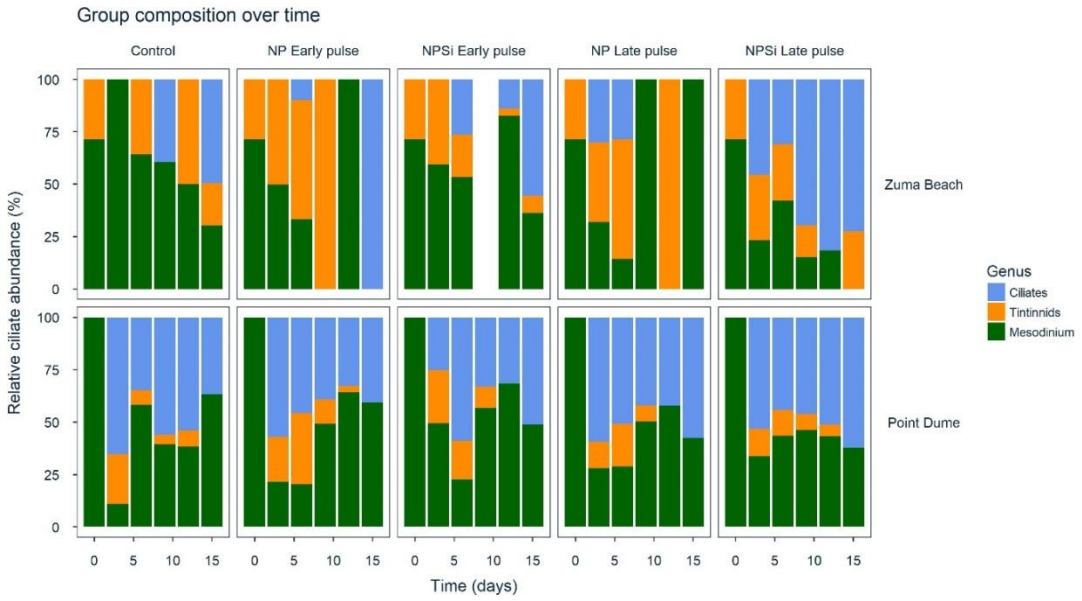


Fig 13 Ciliate composition over time, split up into the two different location, as well as into the different nutrient pulses.

In the communities of Zuma Beach, copepods were only found in a few samples on only a few sampling dates and were not further quantified. Copepod concentrations in the community of Point Dume were higher and more consistent and were therefore assessed by scanning the entire flask. In the different nutrient treatments of Point Dume, copepod concentrations generally followed the same trend as ciliate concentrations at this location, as they increased at first in all treatments. Highest numbers were found on day 12, with the highest mean abundance of 8 individuals (nauplii and adults) per litre in the $NPSi_{Early}$ treatment (Fig. 14). Copepod numbers decreased again at day 15. Concentrations were more stable in the control over time (Fig. 14). However, there were no significant differences in copepod abundance among different treatments and the control (Tab. 3B).

Table 3 *Mesozooplankton abundance responses of the linear mixed models; A: Ciliate abundances, B: Copepod abundances, data were only available for the community of Point Dume*

	Response		Zuma Beach (log+1 transformed)			Point Dume		
		Factor	df	F	p	df	F	p
A	Ciliate abundance	Treatment	4	0.070	0.991	4	0.901	0.468
		Time	1	2.945	0.161	1	2.764	0.172
		Treatment : Time	4	0.374	0.827	4	2.564	*<0.05*

			Point Dume		
		Factor	df	F	p
B	Copepod abundance	Treatment	4	0.314	0.868
		Time	1	2.725	0.197
		Treatment : Time	4	1.548	0.198

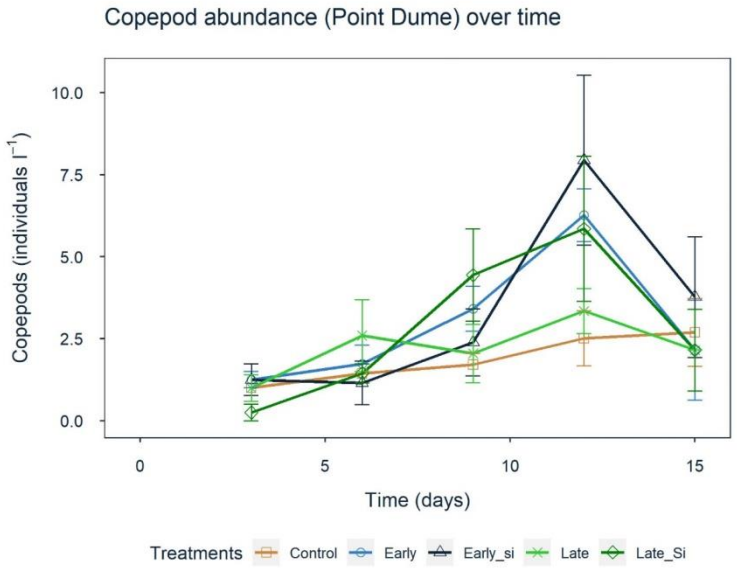


Figure 14 *Mean copepod abundance (individuals per lire) ± SE over time in the community of Point Dume, split up into different nutrient pulses*

Discussion

Both communities showed the same overall biomass trend and increased at the beginning, which was followed by a decrease. Nutrient addition increased chlorophyll *a* content in the treatments compared to the control but did not differ among different nutrient treatments. Overall, it was a consistent pattern that dinoflagellate-dominated communities shifted towards diatom-dominated communities. This shift happened within the first six days but was

independent of the timing, or the composition of the nutrient pulse. While overall trends were similar, the community of Point Dume developed in consistent patterns in terms of biomass and community dissimilarity over time for all treatments. For this location, the LRR increased with increasing dissimilarity, indicating that its changing composition promoted biomass increase. This was not the case for the community of Zuma Beach, which responded in a more chaotic way. These fundamental differences could be related to initial compositional differences of the community, such as high initial *L. polyedra* concentrations at Point Dume.

My experiment revealed that high initial *L. polyedra* concentrations led to an initial increase of *L. polyedra*, while a lower concentration was followed by a direct biomass decrease. However, even with an initial contribution of more than 70% of the total community biomass, *L. polyedra* was not able to successfully compete with co-occurring diatom species and thus decreased. In both communities, *L polyedra* was not able to maintain its biomass, especially the relative contribution to the total biomass, which decreased from the beginning of the experiment on, revealed the rapid bloom termination.

While the composition of taxonomic groups from Zuma Beach and Point Dume showed a strong similarity, species composition revealed some fundamental differences, for instance, regarding the initial dinoflagellate dominance in both communities.

At high initial concentration (70% at Point Dume), *L. polyedra* biomass increased at first. However, this increase was observed both in the control treatment without nutrient addition and in the nutrient pulse treatments, the latter increasing a bit more, indicating that part of the increase must have been driven by other factors than nutrient pulses. After this initial biomass increase of *L. polyedra* in the community from Point Dume, it decreased drastically in both communities. The overall decrease of *L. polyedra* did not appear to be a species-specific response, but rather a dinoflagellate-specific response, as the same pattern was observed for *Gymnodinium* sp., which dominated the community of Zuma Beach at the beginning of the experiment, contributing more than 50% of the initial biomass. Thus, relative dinoflagellate contributions decreased in both communities from the beginning on, whereas diatom dominance increased.

I hypothesized to find more diatoms in treatments subject to the NPSi addition, however as dinoflagellates decreased in all treatments, diatom abundance and relative contribution to phytoplankton biomass drastically increased, which might have negatively influenced both

initially dominating dinoflagellate species due to competition for resources, such as dissolved nutrients. Biomass and species composition in the NP and NPSi treatments did not show strong differences regarding diatom development, indicating that diatoms were not silicate-limited. The SCCOOS Harmful Algal Bloom monitoring program, is a program which monitors harmful algal species and algal toxins at eight piers along the California coastline, in order to improve the understanding of timing, impact and extent of these events on the ecosystem and on humans (SCCOOS, 2018). As part of this program, the nutrient data from the Stearns Wharf station, which has been the closest sampled station to my sample locations (Fig. 1, SCCOOS 2018), were taken four days prior to (5.249µmol Si L^{-1} on 11th Sept. 2017, SCCOOS 2018) and four days after (0.667 µmol Si L^{-1} 19th Sept. 2017, SCCOOS 2018) the beginning of my first experiment. On the starting day of the second experiment, nutrient samples were also taken at Stearns Wharf Station as part of the SCCOOS HAB monitoring (4,136 µmol Si L^{-1} 9th Oct. 2017, SCCOOS 2018). These data reveal that silicate was available, whereas nitrate and nitrite levels, as well as phosphate levels closest to my sampling stations (Stearns Wharf and Santa Monica Pier, source; SCCOOS 2018), were very low (Fig. 15, SCCOOS 2018). Only ammonia concentrations were higher and might have provided an additional N source (Appendix Fig. 2). I, therefore, assume that the addition of Si was insignificant, as the increase of diatoms was triggered by the addition of NP and most likely due to the remaining silicate in the sampled water. Differences in nutrient composition based on Si addition were therefore minor and did not result in any phytoplankton composition differences.

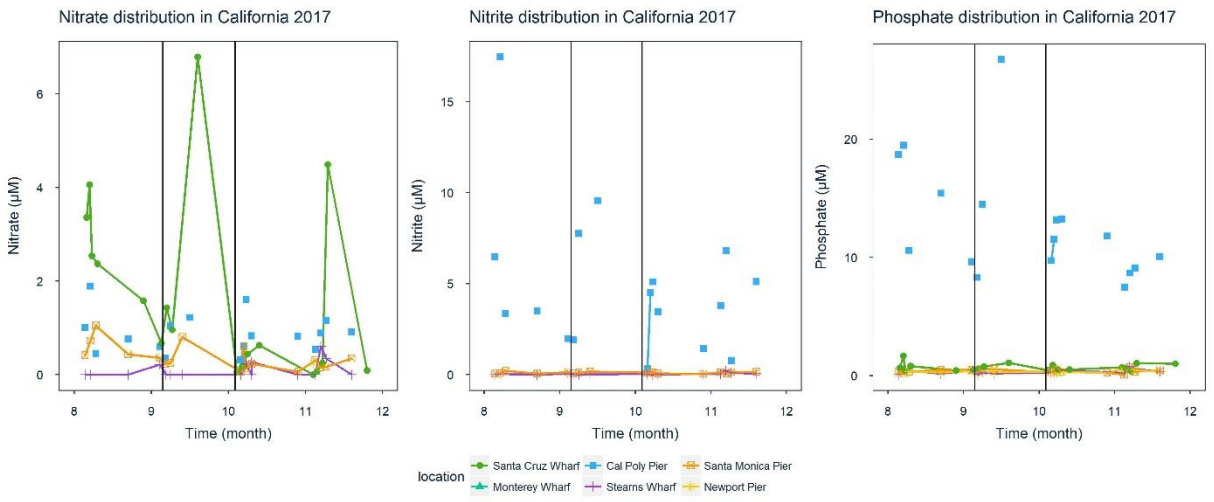


Figure 15 *Nutrient values from the Southern Californian Bight, provided by the SCCOOS HAB Monitoring program (SCCOOS 2018) for nitrate, nitrite and phosphate. Stations have been included in the HAB-Monitoring between August and December 2017*

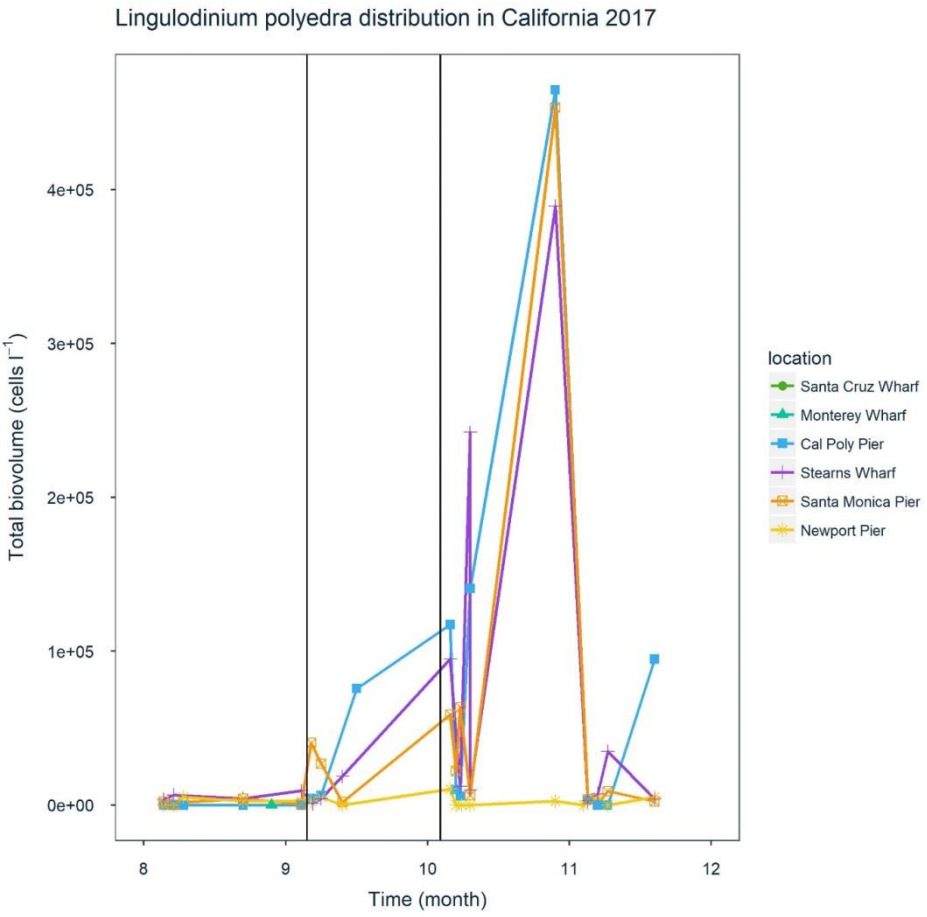


Figure 16 *L. polyedra abundance of the Southern Californian Bight, provided by the SCCOOS HAB Monitoring program (SCCOOS 2018). Stations have been included in the HAB-Monitoring between August and December 2017*

While my data suggest, that nutrient concentrations are a poor predictor for *L. polyedra* blooms, Eppley and Harrison (1975) suggested the opposite for near surface waters via upwelling. Also, *L. polyedra* blooms outside the upwelling season have been associated with nutrient input due to freshwater runoff (Hayward et al., 1995; Kudela and Cochlan, 2000). These, in contrast to my data, opposing findings might be due to the form of the nutrient, such as urea as a nitrogen source. Howard et al. (2014) found that riverine runoff was the main source for urea introduction into the Southern California Bight. In addition, Kudela and Cochlan (2000) showed in an uptake experiment with *L. polyedra*, that maximal uptake rates for either nitrate and ammonium were much lower than the maximal uptake rate of urea-N. This indicates that if urea was available, the nitrogen demand of *L. polyedra* could, to a large extent, be provided by it. Hence, urea might play a role in enabling *L. polyedra* to compete with other species, especially with fast-growing diatoms.

Community composition did not change in dependence of the timing of the nutrient pulse, indicating that nutrient limitation was not strong enough to hamper fast-growing species, such as diatoms in my study, and promote dinoflagellates in treatments with the late nutrient pulse. However, nitrate, nitrite and phosphate were likely (based on SCCOOS data from nearby stations) low since the beginning of the experiment, whereas silicate concentrations in the area were higher. I can, therefore, assume that the effect of nutrient composition might have been stronger on the community and in particular on diatoms, than the effect through the timing of the nutrient pulse.

My findings that dinoflagellates did not benefit from nutrient additions are in agreement with studies on nutrient addition effects on natural phytoplankton communities. Piehler et al. (2004) manipulated the input of nitrogen and phosphorus in natural plankton communities of the southwest basin of Pamlico Sound (North Carolina, USA), where dinoflagellates represented only a very small proportion of the overall population, however still decreased significantly in several of the treatments. Piehler et al. (2004) assumed that dinoflagellates were most likely outcompeted by other phytoplankton species, such as diatoms and cyanobacteria, which is similar to my results. In a mesocosm study in three consecutive years, Kremp et al. (2008) studied the effects of variable nutrient additions and their supply ratios on dominance patterns and species composition of natural spring phytoplankton communities. Similar to my results, they found that diatoms were generally stimulated by an addition of N and P. However, they found that the nutrient addition had no, or even negative effects on the dinoflagellate *Woloszynskia halophila* and that *W. halophil*a bloom dynamics were highly dependent on its inoculum size and the relative initial abundance of diatoms (Kremp et al., 2008). In contrast to my experiment, where diatoms increased rapidly, even at a high initial *L. polyedra* dominance of more than 70%, Kremp et al. (2008) found that at a high inoculum contribution of more than 80% of *W. halophil*a and thus a low initial diatom contribution, diatoms were not able to become dominant before nutrients were depleted. The results of my study suggest that neither nutrient addition nor inoculum size of *L. polyedrum* determined its bloom persistence and development.

Despite the efforts of removing grazing pressure by pre-filtering all samples, ciliates and also copepods were found in samples of both locations. Especially in the community of Point Dume, abundances of both, ciliates and copepods were much higher compared to the

community of Zuma Beach. Grazing through microzooplankton consumers, such as rotifers and ciliates, was shown to play an important role in phytoplankton bloom control (Turner 2006 and citations therein). Different micro- and mesozooplankton species, such as copepods and ciliates such as *Strombidinopsis* sp. *Tiarina fusus* have been found to be able to feed on *L. polyedra* (Jeong et al., 2002, 1999; Teegarden and Cembella, 1996). Stauffer et al. (2017) showed that *Noctiluca scintillans* is able to feed and grow on *L. polyedra.* Busch et al. (in prep.) found that bloom dynamics of *L. polyedra* were highly influenced by the mesozooplankton community composition. In their experiment, they found, that the heterotrophic dinoflagellate *Noctiluca scintillans* strongly controlled *L. polyedra*, whereas abundances of *L. polyedra* were positively correlated with microzooplankton consisting of copepod nauplii and tintinnids. Thus, *L. polyedra* might have been promoted in their study due to competitive release through microzooplankton grazers feeding on other phytoplankton species (Busch et al., in prep.). Grazers can, therefore, play an important role in bloom formation of *L. polyedra*, as they both positively and negatively affect their population dynamics. In my experiment, larger zooplankton grazers were excluded from the experiment, due to the filtration. Micro- and mesozooplankton grazer abundance increased with decreasing dinoflagellate abundance, and especially *L. polyedra* abundance, indicating that the increase of grazers could be explained by grazing on dinoflagellates. In the community of Zuma Beach, *L. polyedra* abundance as well as micro- and mesozooplankton remained low, however, micro- and mesozooplankton increased in the community of Point Dume, while *L. polyedra* abundance decreased. No positive feedback loop of grazing on other species could be found in my experiment, such in the experiment of (Busch et al., in prep.). In contrast, zooplankton numbers even increased in the community of Point Dume.

We did not quantify grazing and can thus not disentangle if zooplankton increased due to grazing on *L. polyedra*, the greater availability of diatoms as food sources, or even due to other interactions. In the community of Point Dume, initial zooplankton consisted of mostly *Mesodinium* sp. and developed into a mixture of mostly unknown ciliates and *Mesodinium* sp.. As different ciliate species have been shown to feed on *L. polyedra* (Jeong et al., 2002, 1999), grazing on *L. polyedra* could potentially explain the interaction of increasing zooplankton and decreasing *L. polyedra* in my experiment. As the *L. polyedra* bloom consisted in the field, it is conceivable, that grazing pressure on *L. polyedra* in the field was weaker due to more complex

food web interactions and thus a stronger competitive release of *L. polyedra.* Overall, in my experiment, grazing might have been more important for the bloom dynamics of *L. polyedra* than nutrient input and initial *L. polyedra* dominance. Hence, filtration likely affected microzooplankton growth through a trophic cascade, releasing microzooplankton from predation and thus indirectly increasing grazing pressure on dinoflagellates.

Despite decreasing *L. polyedra* biomass in my experiment, SCCOOS data from neighbouring stations revealed that the *L. polyedra* bloom persisted over a longer period in the field and even increased its biomass (Fig. 16, SCCOOS 2018). After a short biomass decrease in early October, *L. polyedra* strongly increased its biomass until the end of November. High numbers of *L. polyedra* were found between the Santa Monica Pier and Cal Poly Pier (Fig. 1, 16), which covers a distance of more than 300km. Since the *L. polyedra* dominance decreased drastically over all treatments, but especially in the controls without nutrient additions of Zuma Beach and Point Dume, I can assume that the environmental conditions for dinoflagellates, in general, were more advantageous in their natural habitat compared to laboratory conditions. There are multiple possible explanations for this divergent pattern between my findings and the persisting bloom in the field. This drastic shift from dinoflagellates to diatoms, with the knowledge that the *L. polyedra* bloom continued in the field, might be either through optimal laboratory conditions for diatoms or adverse effects for dinoflagellates.

In order to focus on the effect of nutrient pulses on the community dynamics and HABs, I did not include spatial dynamics into my experiments. Spatial dynamics such as complex ocean currents and hydrodynamic transportation, as well as local environmental factors, had been shown to contribute to the formation and expansion of HABs in the Southern Californian Bight (Bialonski et al., 2016). My previous experiments using nutrient gradients in meta-ecosystems showed that spatially heterogeneous habitats provided different niches and resulted in different phytoplankton community compositions along the gradient, promoting higher dinoflagellate contributions at lowest nutrient concentrations (see Chapter 1 and 2). It is possible that *L. polyedra* needs these spatial properties in order to maintain its bloom. Different studies showed that *L. polyedra* is able to migrate vertically through the water column (Eppley et al., 1968; Heaney and Eppley, 1981; Moorthi et al., 2006). In nutrient-poor surface layers of stratified waters, cells can migrate into deeper layers to take up nutrients from deeper nutrient pools (Eppley and Harrison, 1975). Moorthi *et al.* (2006) demonstrated

that *L. polyedra* aggregates in the surface layers in the morning, whereas cells are more distributed during the afternoon and night. Thus, cells of *L. polyedra* occur heterogeneously distributed, emphasizing the importance of spatial dynamics. In addition, Bollens, Quenette, & Rollwagen-Bollens (2012) reported, that dinoflagellates experience a greater spatial separation from predators, due to an increased dial vertical migration of the dinoflagellates in the presence of the predator (copepod). Experimental units in my experiment were comparably small and did not provide any refuge spaces nor allow dispersal into other habitats. Especially for the community of Point Dume, the effect of grazing might have been stronger, compared to the community of Zuma Beach, as ciliate and copepod numbers were much higher in this experiment. Thus the lack of avoidance behaviour through limiting space might have been more severe in the community from Point Dume.

Previous studies showed that some dinoflagellates are sensitive to water movement and that growing dinoflagellates outside of their natural habitat had been difficult (Dixon and Syrett, 1988; Guillard and Keller, 1984). While I cannot exclude culturing disadvantages for dinoflagellates through the transport as well as the influence of regular sampling, I can assume that this did not restrain *L. polyedra* in particular, since I found an initial increase of *L. polyedra* from Point Dume.

Nutrient pulses, irrespective of nutrient composition, led to an initial biomass increase. This was followed by a decrease and a strong change of community composition, resulting in increased dissimilarity based on genus biomass distributions of the community in comparison to the control. Despite these similarities, striking differences between the LRR based on biomass and the dissimilarity of Zuma Beach and Point Dume were found. The community of Zuma Beach responded similarly to all nutrient pulse treatments; however, the patterns observed were not straightforward, making it difficult to draw any conclusions or predictions from the nutrient pulses regarding community response. The community of Point Dume, in contrast, showed a clear pattern of increasing biomass and dissimilarity over time, where both trends were positive for all nutrient pulse treatments. These strong differences between the responses of both communities might be related to the different initial *L. polyedra* abundances, as the species composition in the community of Zuma Beach was more variable and diverse than the community of Point Dume, which was highly *L. polyedra* dominated. Thus these results indicate how important initial community structures might be for community

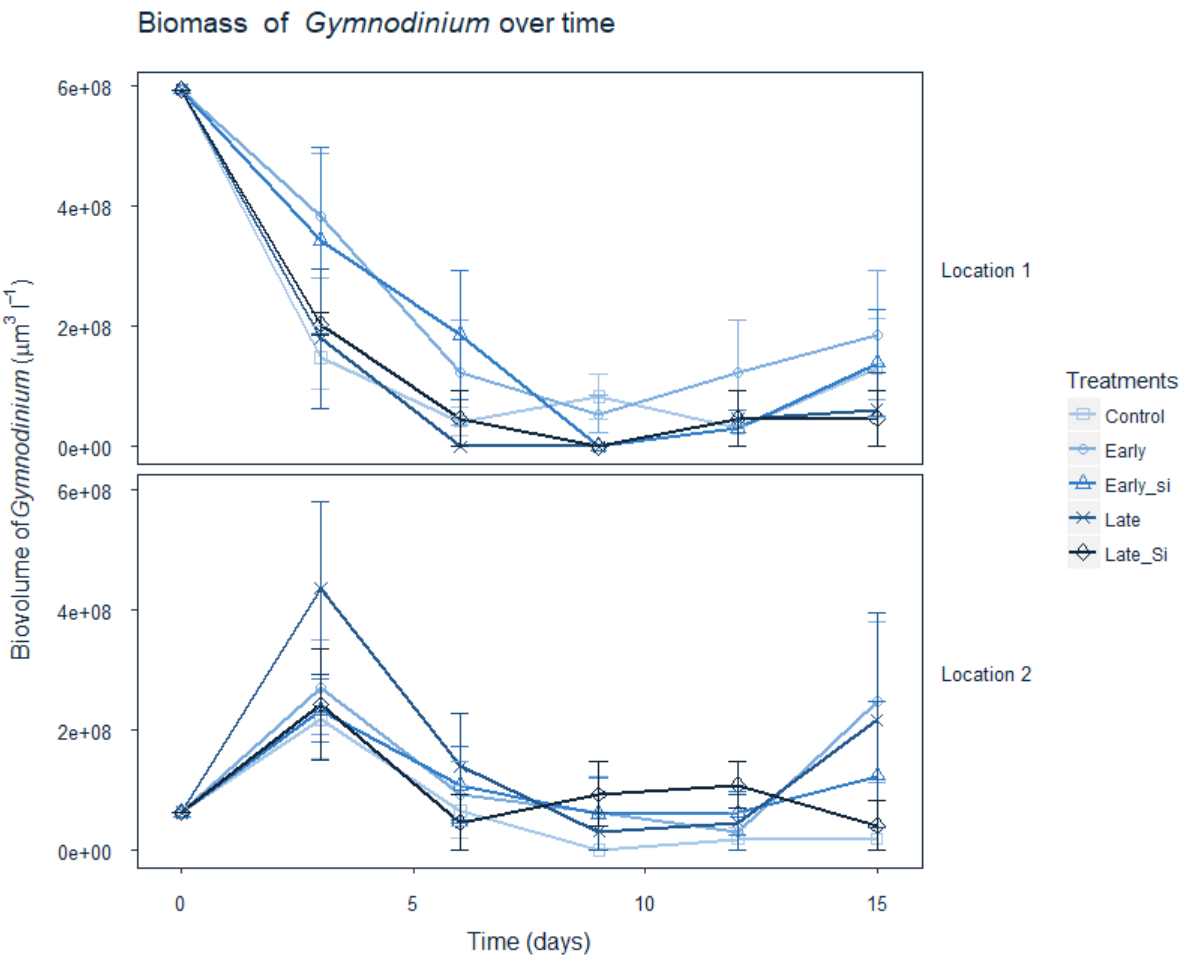
dynamics. Striebel *et al.* (2016) showed in a temperature manipulation experiment with natural and artificially assembled phytoplankton communities that community composition and biomass depended on the initial composition. In addition, Eggers *et al.* (2014) demonstrated in a study on the effect of ocean acidification on marine phytoplankton communities that initial community composition had a greater influence on phytoplankton biomass than elevated CO2. In their study, they suggest that the ratio between different phytoplankton groups (cyanobacteria, diatoms and dinoflagellates) might be crucial for the competitive and thus the functioning of communities, as initial community composition determined competitive and functional outcome at the end of their experiment (Eggers et al., 2014). It is therefore important to emphasize that in my experiment even a similar initial group composition led to different responses to nutrient pulses. However, genus identity showed differences between initial community composition, indicating, that initial community composition might have been a sensitive driver for community responses to nutrient additions and that community parameters, such as species identities or trait diversity might have shaped community dynamics. Functional traits have been found to be good predictors for variations in phytoplankton species responses and thus phytoplankton community structure (Edwards et al., 2013). As I have not assessed functional biodiversity and hence trait variability, I can only assume, that traits such as nutrient kinetics or grazing resistance might have influenced community dynamic and responses in my experiment.

Conclusion

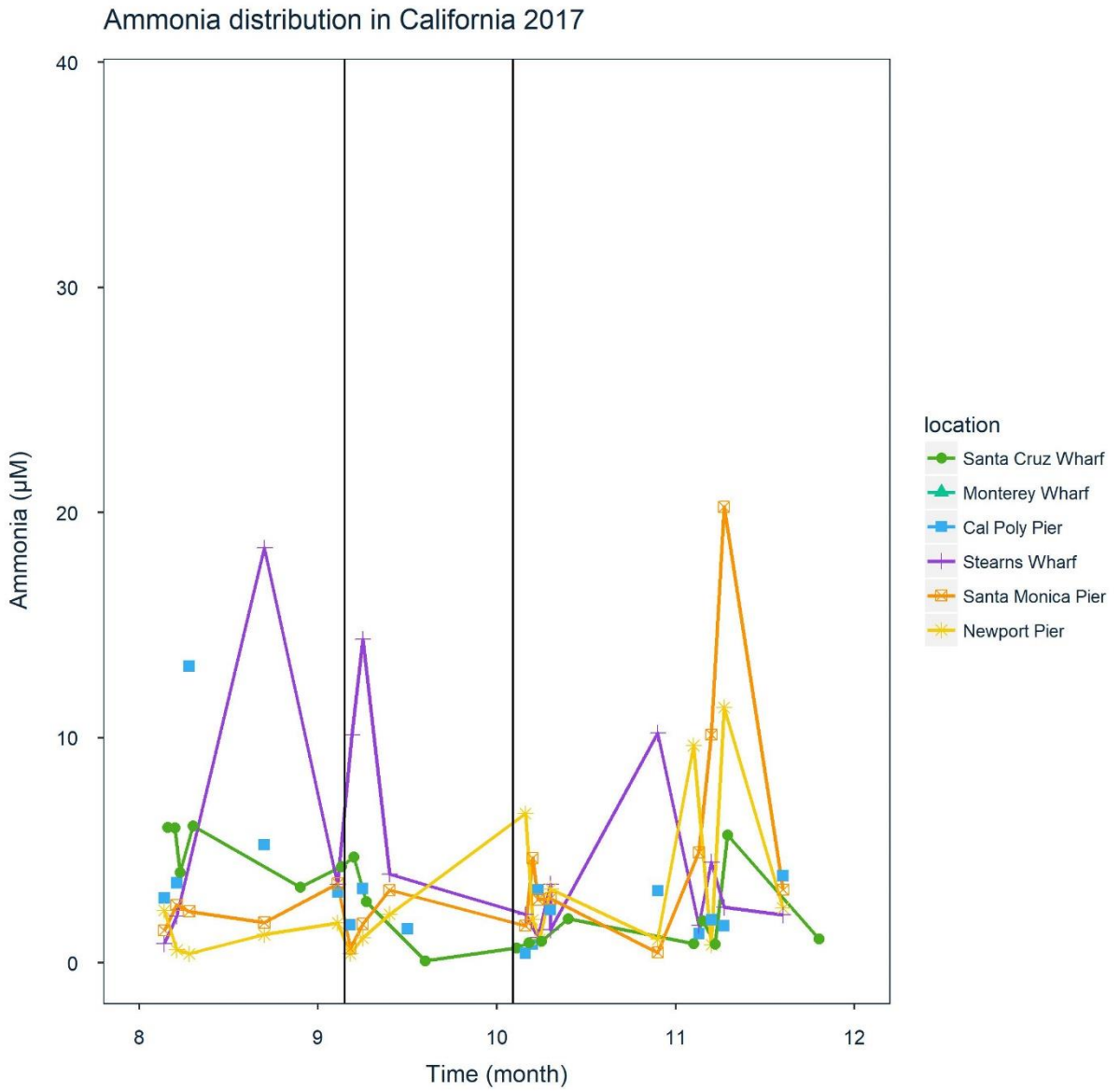
With this study, I demonstrated that neither nutrient pulses of different compositions nor different timing of these pulses promoted dinoflagellate blooms in general and *L. polyedra* in particular, but promoted diatom dominance. I generally found divergent patterns of the community development in terms of biovolume and dissimilarity of the communities from different locations. This shows how important the influences of the initial community structure, and as a consequence, local abiotic and biotic influences that have shaped the different communities, were. Responses on nutrient pulses seem to be hard to predict, and it is conceivable that even stronger variations in groups and species could result in different responses than I found for these two communities.

As nutrient pulses alone did not promote the *L. polyedra* bloom, it is possible, that the combination of nutrient pulses with other local factors might enhance blooms. Grazing of copepods and ciliates in combination with the lack of spatial dynamics might have been more important for *L. polyedra* bloom termination, as it had been reported, that the *L. polyedra* bloom in the field persisted for much longer after my samplings. In order to improve the understanding of *L. polyedra* bloom dynamics, it would be important to test the influence of multiple factors and to study bloom dynamics in the field in more depth. In addition, analytic measurements of nutrient compositions from the sampled areas as well as during the experiment itself might help to explain competition and community dynamics in general.

Appendix



Appendix Figure 1 Mean Gymnodinium sp. biomass (µm³ L⁻¹) ± SE over time, split up into the two different location, as well as into the different nutrient pulses.



Appendix Figure 2 Ammonia values from the Southern Californian Bight, provided by the SCCOOS HAB Monitoring program (SCCOOS 2018). Stations have been included in the HAB-Monitoring between August and December 2017

Appendix Table 2 Overview over the used biovolume of all species/genus, gathered mostly from nordicmicroagae and the encyclopedia of life. Biovolume from specific species was used, if identification was possible.

Genus	Species	BV_min	BV_max	Mean	Source	Based on
Cerataulina	*C. pelagica*	932	119320	60126	nordicmicroalgae	(Olenina et al., 2006)
Chaetoceros		24	5299	2662	nordicmicroalgae	(Olenina et al., 2006)
Cylindrotheca	*C. closterium*	90	396	243	nordicmicroalgae	(Olenina et al., 2006)
Leptocylindrus		707	7850	4279	nordicmicroalgae	(Olenina et al., 2006)
Odontella	*O. aurita*	21760	21760	21760	nordicmicroalgae	(Olenina et al., 2006)
Pseudo-nitzschia		48	10000	5024	nordicmicroalgae	(Olenina et al., 2006)
Skeletonema		125	125	125	nordicmicroalgae	(Olenina et al., 2006)
Guinardia	*G. striata*	49063	49063	49063	nordicmicroalgae	(Olenina et al., 2006)
Navicula		375	14400	7388	nordicmicroalgae	(Olenina et al., 2006)
Rhizosolenia	Common West Coast species:*R. setigera , R. hebatatat, R. Styliformis*	97026	649260	373143	nordicmicroalgae	(Olenina et al., 2006)
Hemialus		16982	16982	16982	eol	(Barton et al., 2013)
Dactyliosolen	*D. fragilissimus*	667	132017	66342	nordicmicroalgae	(Olenina et al., 2006)
Thalassiosira		64	235500	117782	nordicmicroalgae	(Olenina et al., 2006)
Coscinodiscus	Common West Coast species: *C. centralis, C. Granii*	690413	5030292	2860352	nordicmicroalgae	(Olenina et al., 2006)
Fragilaria		69	1313	691	nordicmicroalgae	(Olenina et al., 2006)
Bacteriastrum	Common West Coast species: B. comosum, B. hyalinum	550	197041	98796	eol	(Leblanc et al., 2012)
Thalassionema	*T. nitzschoides*	212	2400	1306	nordicmicroalgae	(Olenina et al., 2006)
Pleurosigma		10838	10838	10838	nordicmicroalgae	(Olenina et al., 2006)
Entomoneis	*E. paludosa, E.ornata,E. alata, E. punctulata*	15100	15100	15100	Possible importance of algal toxins in the Salton Sea, California	(Reifel et al., 2002)

Paralia	*P. sulcata*	3140	3140	3140	nordicmicroalgae	(Olenina et al., 2006)
Ceratium	*C. fusus*	10934	23773	17354	nordicmicroalgae	(Olenina et al., 2006)
Ceratium	*C. tripos*	13644	194618	104131	nordicmicroalgae	(Olenina et al., 2006)
Dinophysis		961	27427	14194	nordicmicroalgae	(Olenina et al., 2006)
Gonyaulax		4179	134628	69404	nordicmicroalgae	(Olenina et al., 2006)
Prorcentrum	*P. gracile*	4123	5941	5032	eol	(Sal et al., 2013)
Prorocentrum	*P. micans*	12953	27632	20293	nordicmicroalgae	(Olenina et al., 2006)
Protoperidinium		1214	304188	152701	nordicmicroalgae	(Olenina et al., 2006)
Gymnodinium		72	69377	34725	nordicmicroalgae	(Olenina et al., 2006)
Oxytoxum		6368	6368	6368	nordicmicroalgae	(Olenina et al., 2006)
Scrippsiella		1442	12764	7103	nordicmicroalgae	(Olenina et al., 2006)
Noctiluca	*N. scintilans*	795925	523333333	262064629	nordicmicroalgae	(Olenina et al., 2006)
Lingulodinium	*L. polyedra*	14130	43986	29058	nordicmicroalgae	(Olenina et al., 2006)
Small_Flagellate	Small Flagellate < 10µm	30	314	172		measured/ calculated as sphere
Smaller_Flagellate	Smaller Flagellate < 3µm	0	28	14		measured/ calculated as sphere
Pyramimonas		24	2304	1164	nordicmicroalgae	(Olenina et al., 2006)
Nephroselmis		17	17	17	nordicmicroalgae	(Olenina et al., 2006)
Cryptophyte	probably *R. salina*	69	125	97	nordicmicroalgae	(Olenina et al., 2006)
Dictyocha		943	943	943	eol	(Sal et al., 2013)
Chattonella		13100	13100	13100	Phytoplankton dynamics in the Salton Sea, California, by Tiffany et al1997–1999 (Tiffany 2007)	(Tiffany et al., 2007)

General Discussion

Harmful algal blooms (HABs) pose a threat to society, as they can cause substantial economic and ecological losses. Thus, a better understanding of bloom dynamics is essential to improve models for future HAB predictions. While HAB prevention might be difficult or not even feasible, the identification of factors promoting HABs is necessary to validate potential natural and anthropogenic stressors and apply management strategies.

While HAB dynamics have been shown to be very complex and influenced by multiple factors, especially nutrient input has often been described to increase the duration and extent of HAB events. Especially upwelling systems exhibit high spatial and temporal nutrient variability and provide high fish production as well as high primary production, including a variety of different HAB species (Fréon et al., 2009; Pauly and Christensen, 1995). Hence, upwelling regions are vulnerable to the effects of HABs, due to their high economic and ecological value. Understanding factors determining bloom formation and propagation is therefore an essential focus in HAB research

The aim of this thesis was to investigate trophic interactions and the propagation of potentially harmful dinoflagellates in a spatial context. In the chapters above, I approached the question of how harmful dinoflagellates are influenced in their propagation and bloom dynamics by nutrients and competition with other plankton species.

With regard to spatial and temporal patterns in upwelling systems, I conducted two meta-ecosystem experiments, including a nutrient gradient. The dinoflagellates *Alexandrium catenella* and *Lingulodinium polyedra* were used in these experiments, because both regularly occur in the Southern California coastal upwelling system. In Chapter 1, I investigated competitive interactions of the bloom-forming dinoflagellates *A. catenella*, whereas I studied

L. polyedra in Chapter 2. The inoculation of the harmful dinoflagellates into different positions along the nutrient gradient into the simplified and assembled community enabled me to conclude propagation patterns of both species. These experiments also provided results about their competitive interactions in different nutrient conditions and associated phytoplankton community structures. Results of both chapters (1 and 2) showed that the harmful dinoflagellate species were able to disperse between habitats of different nutrient regimes and both performed better under lower nutrient conditions, especially when inoculated into this position.

Additionally, I conducted a batch experiment, investigating bloom persistence and population dynamics during an autumn bloom of the dinoflagellate *L. polyedra* along the southern Californian coast. My results showed that the addition of an early or late nutrient pulse did not promote bloom persistence of *L. polyedra*. However, the results indicated, that grazing on *L. polyedra* might have decreased bloom persistence.

Harmful dinoflagellate performance

The results of Chapter 1 and Chapter 2 show differences between the performance of the two harmful dinoflagellates *A. catenella* and *L. polyedra*. *A. catenella* became dominant under lowest nutrient conditions for a limited amount of time (see Chapter 1). Even with an initial biomass advantage, *L. polyedra* was not able to maintain its dominant position in the assembled community and quickly represented a minor portion to the overall phytoplankton biomass (Chapter 2). However, there have been three major differences between the set-ups of both experiments, which might have caused the different outcomes.

First of all, when added into the meta-ecosystem on day 9, both species were set up with the same initial biomass. Due to differences in cell size, different cell numbers of both species were used in the inoculation of each experiment, as *L. polyedra* is larger compared to *A. catenella*. Thus more cells of *A. catenella* have been initially inoculated. Higher cell numbers might have resulted in a competitive advantage of *A. catenella* through mixotrophic feeding. However, Jeong *et al.* (2010) showed that the maximum ingestion rate and the upper prey size limit is positively correlated with the predator size. In addition, studies on both species

showed, that *A. catenella* growth rate was lower when prey was available (*Teleaulax acuta* and *Heterocapsa rotundata*), whereas *L. polyedra* exhibited a higher maximum growth rate when feeding on *Scrippsiella trochoidea* (Blossom et al., 2012; Jeong et al., 2005b), indicating that *L. polyedra* could have been promoted by mixotrophic feeding. As potential prey species differed in my experiments, also feeding characteristics, such as feeding intensity might have varied. Differences in initial cell numbers are considered highly unlikely to be responsible for the different performances of the two HAB species.

Secondly, silicate concentrations differed between both experiments. In Chapter 1, silicate was part of the nutrient gradient and increased together with N and P. In Chapter 2, natural silicate concentrations of the sea water were much higher, and silicate was therefore not incorporated in the nutrient gradient. Due to increasing nutrient availability of nitrogen and phosphorous and thus higher diatom growth at higher positions, also silicate was used in higher proportions. However, silicate concentrations were high in all patches and not limiting at any time during this experiment. As competition for nutrients between diatoms and dinoflagellates was strong, the unlimited availability of silicate in all flasks might have pronounced diatom dominance even more. Diatoms have been shown to have higher growth rates than many dinoflagellates (Litchman et al., 2007), which might have enabled them to thrive even better at high nutrient concentrations. Diatoms were, therefore, able to build up a high biomass quickly, and become the dominant group, whereas dinoflagellates, and *L. polyedra* in particulate, were inferior competitors.

The third difference between both experiments is the species identity or rather differences between their associated traits. Both species exhibit unique traits which might explain the better competitive advantage *for A. catenella* in that kind of meta-ecosystem experiment. Especially the production of allelopathic substances, which can weaken the survival, growth and reproduction of other species, might enable them to thrive in such a highly competitive environment. While *A. catenella* has been shown to produce these substances, *L. polyedra* is not associated with the production of allelopathic substances (Busch, 2016; Granéli et al., 2008; Zhang et al., 2013). However, also other traits, such as light and nutrient affinities or mixotrophy, might differ in their intensities of both species and thus influence their performance.

Trait diversity

In the meta-ecosystem experiments in Chapter 1 and Chapter 2, the harmful dinoflagellates *L. polyedra* and *A. catenella* responded differently in competition with other species along a nutrient gradient. Both dinoflagellates were promoted by low nutrient conditions. Yet, in a direct comparison of both experiment, *A. catenella* represented the stronger competitor, as it was able to dominate the community at lowest nutrient concentration. Species-specific differences were most likely responsible for the different responses, raising the question, why *A. catenella* was more successful under these conditions than *L. polyedra*.

Different species have been shown to exhibit different traits and thus vary in their trait values (Litchman et al., 2012, 2007; Litchman and Klausmeier, 2008). The knowledge of species traits and trade-offs increases the understanding of niche differences between species and hence consequences for species diversity and coexistence, which in turn increase the mechanistic understanding of community dynamics and structure (Chase and Leibold, 2003; Edwards et al., 2013; Litchman et al., 2012).

Already Margalef (1978)used a trait-based approach in his “mandala”, identifying different phytoplankton responses to environmental gradients of turbulence and nutrients. The mandala already emphasised strong dinoflagellate variances, as red tide dinoflagellates appear at low turbulence and high nutrients, whereas other dinoflagellates occur under low nutrient and low turbulence conditions (Margalef, 1978). Only the dinoflagellate genus Alexandrium was classified in low turbulence but intermediate nutrient concentrations (Margalef, 1978).

Recognising that one model can not capture all traits, trade-offs and adaptations, such a conceptual approach as the mandala simplifies and helps to compare, relate and contrast phytoplankton functional types in their environment (Glibert, 2016). Thus, based on this concept, Glibert (2016) diversified Margalef’s mandala and included a total of twelve responses, which can also be identified as effect traits. However, similar to the original mandala, the new mandala categorises only two different kinds of dinoflagellates: bloom-forming and low biomass dinoflagellates. While such a scheme provides important information about general dinoflagellate responses to environmental factors, species-specific trait variances are not covered.

In the following section, I will discuss functional diversity and thus trait diversity of the harmful dinoflagellate species *A. catenella* and *L. polyedra*. The variety of traits in phytoplankton is exceptionally high, and it is not possible to consider all traits. Therefore I will focus on the twelve effect traits based on the revised phytoplankton mandala of Glibert (2016), to identify differences between both dinoflagellates. For the sake of completeness, I will discuss all parts of the mandala, although this partly exceeds the scope of this research and can therefore not.

Nitrogen forms and the relative availability of inorganic nitrogen and phosphorus (1&2)

Upwelling systems provide high amounts of dissolved nutrients, which are moved from deeper waters to the surface waters, with high amounts of nitrate (NO_3^-) as the primary nitrogen source (Fréon et al., 2009; Glibert et al., 2016). However, also anthropogenic inputs contribute a large portion to the increased nutrient load, including other nitrogen forms. Urea and Ammonium (NH_4^+) can, for instance, be increased through runoffs from wastewater treatment plants, or due to aquaculture operations (Bouwman et al., 2013; Glibert et al., 2011). These nitrogen forms can be taken up and metabolised differently by phytoplankton (Fréon et al., 2009; Glibert et al., 2016). In addition, in many aquatic ecosystems, the N:P ratio is increasing due to an increasing nitrogen input through N-based fertilisers and a stronger P management and control, (Glibert, 2016 and references therein).

In all three chapters, only the inorganic nitrogen form NO_3^- was used in the nutrient gradient or the nutrient pulses. Hence, based on my study, I cannot distinguish between the effect of organic or inorganic nutrient forms and whether the dinoflagellate species would have favoured a specific nitrogen source. Isolated *A. catenella* cells from the Thau lagoon (northern Mediterranean) have been analysed by Collos *et al.* (2004) for their growth and uptake characteristics of nitrate, ammonium, and urea (Tab. 1). Low concentration uptake was fastest for ammonium, which also inhibited nitrate uptake when both were present (Collos et al., 2004). Urea uptake was fastest at high concentration, and its uptake was overall faster than that of nitrate (Collos et al., 2004). Kudela and Cochlan (2000) analysed similar uptake kinetics of a red tide bloom off southern California consisting of almost only *L. polyedra* cells (Tab. 1). Their results showed that *L. polyedra* had a higher maximum uptake rate for urea compared to nitrate or ammonium, indicating, that urea could provide a high proportion of its nitrogen

demand at ambient urea concentrations (Kudela and Cochlan, 2000). Kudela and Cochlan (2000) demonstrated that natural assemblages of *L. polyedrum* could exhibit higher affinities for reduced nitrogen than expected from literature (Tab. 1).

Urea might be an important nitrogen source for *L. polyedra*, whereas ammonium was the preferred nitrogen source for *A. catenella* (Collos et al., 2004; Kudela and Cochlan, 2000). The choice of the nitrogen form for experiments, might be crucial for species competition for this resource.

Table 1 Uptake characteristics of Alexandrium catenella and Lingulodinium polyedra. Maximum uptake rate and half-saturation constant for both harmful dinoflagellates dependent on three different nitrogen forms. (References: [1]Collos *et al.*, 2004; [2]Collos *et al.*, 2007, [3]Kudela and Cochlan, 2000*)*

	N source	*A. catenella*	*L. polyedra*
Vmax (Maximum uptake rate; µg-at N $cell^{-1}$ h^{-1})	NO3	[1]0.003-0.047 (culture), [1]0.024 (field)	[3]0.480 *10^{-6}
	NH4	[1]0.026 (culture), [1]0.064 (field)	[3]1.01 *10^{-6}
	Urea	[1]0.025 (culture), [1]0.061 (field)	[3]1.321 *10^{-6}
Ks (Half-saturation constant; µg-at N L^{-1})	NO3	[1]0.6-28.1 (culture), [1]4.6 (field)	[3] 0.467
	NH4	[1]2.0 (culture), [1]8.4 (field), [2]0.5,[2]6.2	[3] 0.989
	Urea	[1]28.4 (culture),[1]43.9 (field)	[3] 0.586

In nature, both species might profit from increasing ammonium and urea concentrations through anthropogenic influences and thus an increased N:P ratio. In the meta-ecosystem experiments, I used a nutrient gradient with increasing amounts of nitrogen and phosphorus, but with a constant N:P ratio. I can therefore not discuss the influence of N:P ratios on the dinoflagellate performance in my experiments. However, different studies have investigated the effect of N:P ratios on dinoflagellates. Murata et al. (2012) showed that the cell growth of *Alexandrium tamarense* was correlated with concentrations of nitrogen and phosphorus and changed with changes in the ratio. In addition, they showed that changes in N:P ratios affected the toxicity of *A. tamarense* (Murata et al., 2012). A direct comparison of effects from nutrient ratios between *A. catenella* and *L. polyedra* has not been done. Gülzow et al. (2019) used a similar meta-ecosystem setup such as in Chapter 1 and Chapter 2, and established a spatial resource gradient with a countercurrent of nitrogen and phosphorus to investigate how spatial resource gradients and connectivity affects stoichiometry, community composition

and resource use efficiency of marine phytoplankton. Such a countercurrent set-up could be adapted to HAB research and could reveal how competition and stoichiometry of HAB species change across a gradient of N:P ratios and might thus help for future predictions concerning HAB dynamics in changing nutrient environments.

Light adaptations and feeding modes (autotrophy vs mixotrophy) (3)

Light represents an essential resource for aquatic ecosystems, as many phytoplankton species rely on photosynthesis to acquire energy. However, in contrast to the relatively clear separation of plants and animals in terrestrial species, aquatic organisms can be more complex than just phototrophic (producing energy and carbon using light and inorganic compounds) or heterotrophic (dependent on preformed organic material) (Caron, 2016). Mixotrophic nutrition is widespread among plankton and occurs in many different groups, size classes and different forms, as some species need photosynthesis only in the absence of food, whereas others are almost completely autotrophic (Caron, 2016; Jones, 2000). Upwelling regions exhibit a complex interaction of nutrient and light dynamics, as the system is rather light limited in high nutrient and well-mixed waters but nutrient limited in stratified waters, where light availability is higher (Hood et al., 1992). Due to the ever-changing conditions in upwelling regions through turbulence, light, nutrient and temperature changes, these systems provide multiple niches which can be occupied by species using different strategies, such as mixotrophy (Lamont et al., 2014; Vidal et al., 2017).

The revised mandala by Glibert (2016) incorporates a scale for mixotrophy as almost all phytoplankton classes except for cyanobacteria and diatoms have to some extent a mixotrophic capability (Flynn et al., 2013). Hence, mixotrophy is an important trait, especially in the light of my experiments, where competition between diatoms and dinoflagellates played a strong role.

Both dinoflagellates, *A. catenella* and *L. polyedra,* have been shown to be mixotrophic. Mixotrophic feeding of *L. polyedra* has been demonstrated for bacteria, cyanobacteria, dinoflagellates and diatoms (Jeong et al., 2005b; Seong et al., 2006; Yoo et al., 2009; Zhang et al., 2013). Mixotrophic feeding of *A. catenella* has been more challenging to measure, and in many experiments, adverse effects on the prey species have rather been due to allelopathic substances (Blossom et al., 2012; Zhang et al., 2013). In a comparison of mixotrophy and

phototrophy of *L. polyedra*, found Jeong *et al.* (2005), that under a 14:10 h light:dark cycle of 50 µE m^{-2} s^{-1}, maximum specific growth rate as mixotroph (light and food available) ranged between 0.254 and 0.303 d^{-1}, depending on the prey species, whereas maximum specific growth rate without prey ranged between 0.157 and 0.182 d^{-1}. When inoculated with *Teleaulax acuta, A. catenella* exhibited a lower maximum growth rate of 0.04-0.06 d^{-1}. However, no feeding was shown (Blossom et al., 2012). In contrast, in a pre-experiment with pairwise culturing of *A. catenella* with all four community species, I found that *A. catenella* fed on *Rhodomonas abbreviata*, but no growth rates or ingestion rates have been measured.

Dinoflagellates size has been shown to be positively correlated with the maximum ingestion rate of mixotrophic feeding (Jeong et al., 2010). Considering the larger size of *L. polyedra*, it is not surprising, that higher maximum growth rates have been found for *L. polyedra* when inoculated with potential food. Hence, *L. polyedra* growth could have been promoted more by mixotrophic feeding than *A. catenella.*

Cell motility (4)

Cell motility, in general, can range from swimming cells (flagellated cells) to no motility at all, including sinking and floating strategies as well as vertical migration. Dinoflagellates are, as their name already suggests, flagellated cells. They are motile species, as they exhibit direct motion in response to different factors such as light or nutrients (Cullen and Macintyre, 1998; Heaney and Eppley, 1981; Moorthi et al., 2006).

Vertical migration involves a circadian rhythm, geotaxis and a chemosensory behaviour and allows species to move to deeper waters during the night to take up nutrients and avoid predation, whereas cells move to shallower water during the day (Granéli and Turner, 2006). Both species, *A. catenella a*nd *L. polyedra,* exhibit vertical migration. *A. catenella* has been shown to migrate light and nutrient dependently, aggregating at 1-2m depth (~30% of summer sunlight) when nutrients were not limited, but migrating in deeper areas (10-15% of the summer sunlight) under nutrient limitation (Anderson and Stolzenbach, 1985). Nutrient and light-dependent migration patterns have also been found for *L. polyedra* migrations (Heaney and Eppley, 1981; Moorthi et al., 2006). Vertical migration enables both dinoflagellates to thrive in stratified conditions, as they can take up nutrients from deeper layers and might

enhance their competition, especially with diatoms. However, no direct comparison of the motility of both dinoflagellate species has been done.

Environmental turbulence and temperature (5&6)

The revised mandala includes turbulence and temperature which are acting in opposite directions; low turbulence is associated with high temperature and vice versa (Glibert, 2016).

Dinoflagellates have been found to be sensitive to small-scale turbulence, as they exhibit a variety of different, mostly negative, responses to turbidity, including alterations of the morphology, swimming behaviour, and RNA and DNA cell content, a decrease of the net growth rate, or cell death (Berdalet *et al.*, 2007 and citations therein). As both meta-ecosystem set-ups included continuous mixing, these small scale-turbulences could have influenced both dinoflagellates. Sullivan and Swift (2003) showed in an experiment with two turbulence treatments, that *A. catenella* was unaffected by turbulence, whereas *L. polyedra* even had increased net growth rates in high turbulence treatments. Juhl et al. (2000) found different results, showing that *L. polyedra* growth was lower under rotation, compared to a still control chamber. *L. polyedra* appears to be more sensitive to turbulence than *A. catenella*.

In nature, turbulence often occurs together with changes of temperature, especially in upwelling systems. Deep cold water mixes with warm surface waters, decreasing the water temperature in the upwelling period, whereas surface water is warmer under stratified conditions, in relaxation periods. Laabir *et al.* (2011 and citations therein) showed that optimal growth of *A. catenella* ranged between 10 and 27°C, depending on the study, while in their experiments the strain ACT03 could grow between 15 and 30°C and had highest growth rates at 27°C. In an experiment with three different temperatures (10, 15, 20°C) and five different irradiances, *L. polyedra* exhibited the highest growth rate at 20°C (Meeson and Sweeney, 1982). My experiments were conducted at 17.5-18.0°C, which is in the growth range of both species, but appears to be below the optimal temperature of both

Pigmentation (7)

The revised mandala has an axis for pigment quality which ranges from higher relative proportion of carotenoids to a higher relative proportion of phycobiliproteins and chlorophylls (Glibert, 2016). Different pigment compositions of phytoplankton result in the utilisation of different parts of the light spectrum (Stomp et al., 2004). They are therefore an essential trait for light harvesting processes and hence for the biomass production.

Dinoflagellates appear to be red or brownish coloured, which already indicates their high rate of carotenoids compared to many other groups. *A. catenella* has been shown to contain different pigments, with chlorophyll *a* as the major component, and intermediate occurrence of chlorophyll c_2, peridinin and diadinoxanthin, and some other minor pigments (Carreto et al., 2001). Chlorophyll *a* and *c* were identified as the only green pigments of *L. polyedra,* whereas peridinin was the predominant carotenoid (Sweeney et al., 1959). In addition, dinoxanthin, diadinoxanthin, diatoxanthin and ß-carotene were found in *L. polyedra* (Knoetzel and Rensing, 1990 and references therein). In a comparison of the pigment composition of 64 dinoflagellate species (122 different strains), Zapata *et al.* (2012) also included two strains of *L. polyedra* and three strains of *A. catenella (Tab. 2)*. Major differences between both species were found in the ratio of peridinin to chlorophyll *a* and to chlorophyll *c2*, which was higher in *L. polyedra*, whereas the ratios of diadinoxanthin and dinoxanthin to chlorophyll *a* were slightly lower, compared to *A. catenella*. Peridinin absorbs light in the range of 470-550 nm (blue-green light), which is outside the accessible range of chlorophyll molecules (Hofmann et al., 1996).

Table 2 Molar pigment ratios to chlorophyll and their variability in chloroplast type 1 for A. catenella und L. polyedra; Pigments: Peridinin (Peri), Diadinoxanthin (Diadino), Dinoxanthin (Dino); modified after Zapata *et al.*, 2012

Species	Strain	Peri : Chl *c2*	Peri : Chl *a*	Chl *c2* : Chl *a*	Chl *c1* : Chl *a*	Diadino : Chl *a*	Dino : Chl *a*
A. catenella	AT02	3.05	0.85	0.28	0.00	0.63	0.24
A. catenella	VGO609	3.00	0.84	0.28	0.00	0.43	0.39
A. catenella	AL96	2.90	0.64	0.22	0.00	0.28	0.14
L. polyeda	LP9V	4.12	1.10	0.27	0.00	0.37	0.19
L. polyeda	LP4V	3.85	1.11	0.29	0.00	0.37	0.20
Mean							
A. catenella		2.98	0.78	0.26	0.00	0.45	0.26
L. polyeda		3.99	1.11	0.28	0.00	0.37	0.20

Cell size (8)

Phytoplankton cell size is extremely diverse and ranges over several orders of magnitudes. It can be influenced by different factors, such as *L. polyedra*, whose cell size has been shown to be influenced by temperature and irradiance (Meeson and Sweeney, 1982). In addition, cell size affects other traits, such as nutrient uptake or grazing. For example, mixotrophic ingestion rate and the maximum prey size of mixotrophic dinoflagellates has been shown to be positively correlated with cell size (Jeong et al., 2010)

Compared to the entire size range of phytoplankton, both dinoflagellates are relatively similar in size. However, in direct comparison, both species differ in their size range, as *L. polyedra* is bigger than *A. catenella*. In my experiments, *A. catenella* had a mean length of 27µm (range: 29 -26 µm) and mean width of 28µm (range: 23- 38µm), whereas *L. polyedra* had a mean length of 37µm (range: 26-45) and mean width of 42µm (range: 36- 55µm). As both meta-ecosystems were set up with similar biovolume, differences in cell size were considered.

In addition, some species form chains, which can be advantageously under certain conditions. For instance, cell chains have been shown to increase swimming speed, which potentially promotes bloom formation (Fraga et al., 1989; Sohn et al., 2011). *A. catenella* often forms chains of 4, 8, 16 or more cells, whereas *L. polyedra* cells appear solitary (Hansen and

Moestrup, 1998; Lindström et al., 2017). Hence, *A. catenella* might benefit from chain formation, as increased swimming speed could enhance other traits, such as vertical migration in natural systems. But also in the meta-ecosystem, dispersal was an important factor, which could have been promoted by faster swimming of *A. catenella* chains.

Relative growth rate and ecological strategy (r vs K) (9&10)

Already the original mandala incorporated the ecological concept of r vs K strategies, which describes the trade-off between fast growth and productivity on the one side and maintenance and efficiency of resource acquisition on the other side (Glibert, 2016; Margalef, 1978). In the "old" and the revised mandala, diatoms are described as r strategists, whereas dinoflagellates represent K strategists. However, also between dinoflagellates, there are differences between these strategies. As a high density bloomer, *L. polyedra* belongs closer to the r strategists than *A. catenella*. Yet, even with an overall biomass increase, *L. polyedra* did not form a high-density bloom in my experiment. Hence, a combination of unfavourable conditions, such as discussed before, e.g. lack of vertical migration, intense competition for nutrients or the available nutrient form could have resulted influences its performance.

In my meta-ecosystem experiments, growth was influenced by dispersal and semi-continuously removal through sampling. Growth rates are highly influenced by abiotic and biotic factors, such as nutrient and light availability, but also by grazing. In a study by Jeong *et al.* (2005), *L. polyedra* exhibited a growth rate of 0.182 d^{-1}, whereas *A. catenella* had a much lower growth rate in a different study of 0.06- 0.07 d^{-1} (Blossom et al., 2012). Collos *et al.* (2004), however, found a maximum growth rate of 0.33 d^{-1} for *A. catenella*, indicating that growth of this dinoflagellate might be influenced by environmental factors, as especially light differed strongly between both experiments, with much lower light intensity, where lower *A. catenella* growth rates were found.

Overall, growth rates might not differ strongly between both species. But *L. polyedra* is known for its high biomass blooms, wherefore it is considered closer to the r strategists side than *A. catenella* (Fig. 1)

Relative production of biotic compounds such as toxins or reactive oxygen species (ROS) (11)

Different compounds such as toxins, allelopathic substances or ROS can negatively influence surrounding predators, competitors and even higher trophic levels. Many phytoplankton species have been shown to generate reactive oxygen species (ROS), such as, e.g. superoxide, which can cause mucus production and hence fish gill tissue injuries (Oda et al., 1997). ROS are a common metabolic byproduct, which is known to damage DNA, proteins and lipids (Lesser, 2006). Mardones *et al.* (2015) found a strong influence of ROS in combination with fatty acids docosahexaenoic acid and potentially other polyunsaturated fatty acids during an *A. catenella* fish-kill event in Chilean fjords, which are believed to be responsible for the fish gill damage. To my knowledge, no study has investigated ROS production of *L. polyedra*, wherefore I cannot compare the ROS effects of both species.

Both dinoflagellates used in my experiment have previously been shown to produce toxins. *A. catenella* is a saxitoxin producer, a potent toxin, which can severely harm other species and can cause paralytic shellfish poisoning outbreaks in humans (Grattan et al., 2016; Jester et al., 2009a). *L. polyedra,* in contrast, produces yessotoxin, which had been shown to have lethal effects on mice, but has not had any toxic effect on humans, nor on mammals in the Southern California Bight (Aune et al., 2002; Caron et al., 2010). Toxin content has also been shown to vary, depending on environmental factors and the growth phase. For instance, *A. catenella* toxin content and concentration is influenced by temperature and salinity (Laabir et al., 2013). Additionally, *A. catenella* produces allelopathic substances with a lytic ability to harm potential competitors and consumers (Arzul et al., 1999; Busch, 2016). As it can weaken survival, growth and reproduction of other species, it might enable *A. catenella* to thrive in strong competitive environment. *L. polyedra*, in contrast, has not been shown to produce any allelopathic substances (Busch, 2016).

*O*verall A*. catenella* appears to have stronger effects on surrounding species, as it produces a variety of chemically harmful substances. As competitive interactions between different species were strong in the meta-ecosystem experiments, the ability to produce allelopathic substances and ROS could be responsible for the better performance of *A. catenella*, compared to *L. polyedra.*

The fate of the production in terms of grazing (12)

The outermost layer of the revised mandala describes the fate of production in the food web which is directly connected to the relative strength of micro vs macro-grazing control (Glibert, 2016). The potential grazers provide information on the pathway and if the production will rather cycle through the microbial loop and thus regenerate or if the production will lead to new production as it moves up the food web (Glibert, 2016).

Different grazers feed on *A. catenella*, such as the lobster krill *Munida gregaria* (Mackenzie and Harwood, 2014) and the heterotrophic dinoflagellate *Noctiluca scintillans* (Stauffer et al., 2017). In addition, results from Estrada *et al.* (2008) indicate ciliate feeding on *A. catenella*, including a high proportion of tintinnids, during a microcosm experiment. *A. catenella* often affects higher trophic levels; this effect can be due to grazing which can lead to, e.g. a decreased growth rate of the grazer (Stauffer et al., 2017) or through the production of adverse compounds, as discussed earlier. As their effect on higher trophic levels is often negative and hence does not increase new production of higher trophic levels, *A. catenella* production rather leads to the regeneration via the microbial loop.

Grazing on *L. polyedra* had been found for a variety of species, including the dinoflagellate *N. scintillans* (Busch, 2016; Stauffer et al., 2017) and micro-and mesozooplankton such as copepods (Teegarden and Cembella, 1996) or the ciliates *Strombidinopsis* sp. and *Tiarina fusus* (Jeong et al., 2002, 1999). Even though direct grazing was not assessed in my experiment, result from Chapter 3 indicated that *L. polyedra* decrease was promoted by micro- and mesozooplanktonic grazing. In comparison of both species, it appears that *L. polyedra* might provide more biomass for higher trophic levels, whereas *A. catenella* might play a more significant part for the microbial loop. However, it must be considered, that *L. polyedra* can form massive blooms and that even if grazing removes a substantial part of the biomass, a large proportion often decays and leads to severe oxygen depletion. Hence, *L. polyedra* plays an important role in both pathways.

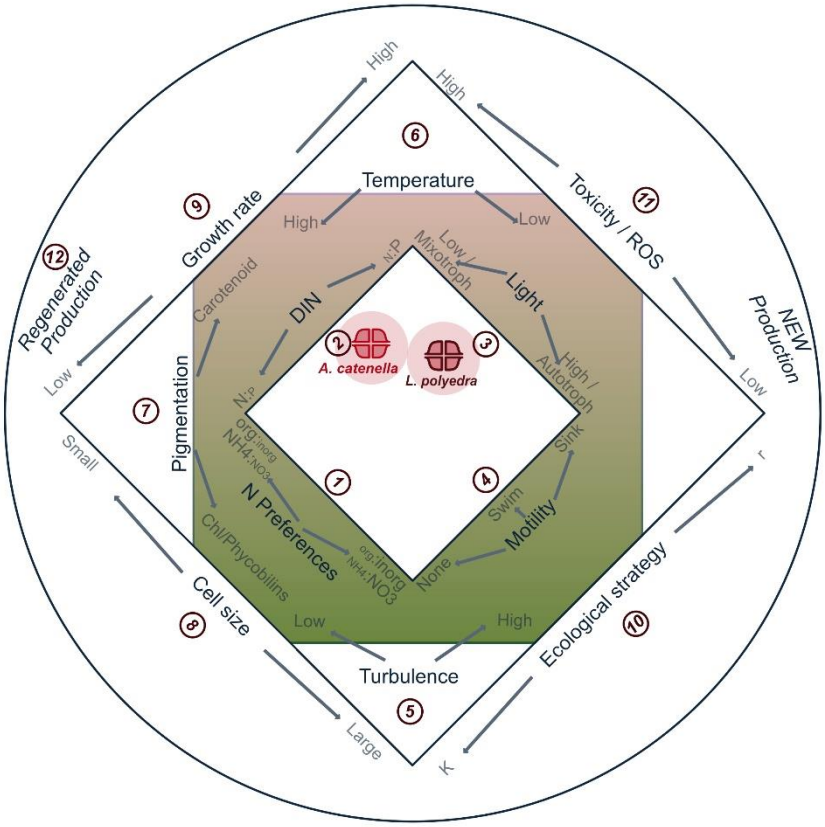


Figure 3 Phytoplankton mandala modified after Glibert (2016). *Phytoplankton functional types or functional traits are assigned along 12 axes (indicated by circled numbers). Lingulodinium polyedra and Alexandrium catenella are aligned along all axed. The axes represent: (1) The preferred nitrogen forms used by the dinoflagellate from NH_4^+ to NO_3^- and from organic to inorganic forms; (2) Gradient of dissolved inorganic nutrient (DIN) with ranging N:P ratios. The middle represents the Redfield ratio; (3) Light adaptation and the tendency of mixotrophy vs autotrophy; (4) Cell motility ranging from no or only very little motility over swimming behavior to sinking and floating strategies of vertical migration; (5) Turbulence ranging from low to high; (6) Temperature ranging from high to low; (7) Pigmentation of cells with higher proportion of carotenoids vs. chlorophylls and/or phycobiliproteins; (8) Cell size ranging from small to large cells; (9) Growth rate from low to high; (10) Ecological strategies: K vs r; (11) Capability to produce toxins and/or other bioreactive compounds such as reactive oxygen (ROS) plotted from high to low; (12) Relative strength of micro- vs. macrozooplankton grazing and the tendency of the production to regenerate and cycle through the microbial loop or generate new production*

Trait comparison

Overall, trait comparison of *L. polyedra* and *A. catenella* exhibited differences between both species. Their different trait characteristics enables them to occupy specific niches and to thus thrive under certain conditions (Fig. 1). Assigning both dinoflagellates to all twelve axes remain complicated, as trait interactions and trade-offs might influence species responses. Multiple axes share the same level, making specific differentiations difficult. For instance, *A. catenella* has been shown to produce more toxins compared to *L. polyedra*, whereas *L. polyedra* appears

to be better adapted to low light, using mixotrophic feeding. However, also cell size is part of the same level, wherefore I neglected the difference of light adaptations between both species and focused more on the other factors nitrogen preference, cell size and toxicity.
It became clear that traits are highly connected and influenced by other traits and that the success of a single species, such as *A. catenella* under lowest nutrient conditions cannot be attributed to one single factor. Instead, a combination of traits under specific environmental conditions can promote blooming. In addition, there might have been other traits, not discussed further, which could have influenced the sensitive interplay of species in my experiment. Hence, changes in environmental factors, such as temperature, light or nutrients might change species performance. Species traits should, therefore, always be considered in the ecological context.

As major primary producers, phytoplankton can be sensitive to global environmental change, which drives different changes in species responses. The combination of genetic adaptation, species sorting, and phenotypic plasticity can contribute to these responses (Litchman et al., 2012). In this context, it is also important to consider that *A. catenella* and *L. polyedra* used in the meta-ecosystem experiment were single strains. Single strain result may vary, compared to population dynamics, as natural populations can be highly complex. In addition, many of the trait observations, discussed above, have been made in single experiments and in many parts with single strains only. Thus, it remains unclear how much variance occurs in each trait of each species, and hence how big their actual trait space is (Fig. 1, indicated by circles). Tillmann *et al.* (2009) demonstrated the intra-population variability of different strains of one *Alexandrium tamarense* population could be high, as they found variations in their allelochemicals activity, specific growth rate and toxin content. Strains are most likely not distributed equally in a population and, depending on previous and current conditions, certain strains might perform better than others. Hence, environmental changes might influence populations of similar species differently, depending on their pre-condition or initial population composition.

The meta-ecosystem approach

The meta-ecosystem setups presented in this study were the first approach to study HAB dynamics in such a spatial context, allowing dispersal along a nutrient gradient. Results of both chapters (1 and 2) showed that dispersal influenced phytoplankton community composition and nutrient distribution of all patches. Both harmful dinoflagellate species were able to disperse between habitats of different nutrient regimes.

Similar spatial distributions, as in my study, have also been found in nature. Mercado et al. (2014) found a strong spatial diatom to dinoflagellate gradient from the coast to offshore waters in the Western Mediterranean Sea, which was accompanied by a decreasing nutrient gradient and mostly influenced changes in diatom abundance. Hence, meta-ecosystems provide a good method to capture spatial dynamics.

The overall results need to be considered in the light of the meta-ecosystem context, where cells disperse through the system. When cells are inoculated into a specific position at the beginning of the experiment, there is a trade-off between the local increase through growth and the decrease through dispersal via step-wise introduction into neighbouring patches. Hence, when inoculated into unfavourable conditions, growth will be low or even non-existent. Thus, low cell numbers will disperse into adjacent patches, leading to even lower cell numbers in all patches and as a result demanding conditions for a successful competitive performance of that species. In contrast, when a species is inoculated into favourable conditions, growth is high. Thus more cells will disperse, but also more cells will remain in the initial patch and strengthen their prevalent position. In Chapter 1, the treatments without dispersal support this concept. When *A. catenella* cells could neither disperse nor additional nutrients and cells from other patches invade, I found a much stronger dominance of *A. catenella* under lowest nutrient concentrations. Already only two minutes of daily dispersal made a huge difference for community dynamics (Chapter 1).

As Chapter 1 provided valid data about the influence of dispersal, the choice of a different dispersal time would have changed overall community dynamics. Especially higher dispersal rates could have led to the assimilation of communities, whereas a lower dispersal rate could have enhanced local differences. These results showed how sensitive communities could react to dispersal and thus how important spatial connectivity is for community development.

In addition, the meta-ecosystem setup provides the possibility to consider different spatial scales, such as in Chapter 1 and 2, where I analysed effects on a local and regional scale (one single flask vs all five flasks together). Results of both Chapters showed that responses varied depending on the analysed scale. Hence, this study emphasises, that the choice of scaling in experimental and field sampling should be made with thoughtful considerations of the spatial properties and the research question.

Influence of community composition on HAB dynamics

In Chapter 1 and 2, the experiments were conducted with an artificially assembled community of potentially co-occurring species from the Southern Californian Coast. I used a complex spatial set up with five spatially distributed nutrient conditions and assessed competition and bloom dynamics in a simple community. In Chapter 3, in contrast, I studied nutrient input, as single pulses only, in more complex communities, which were naturally sampled, only excluding larger species (> 200 µm).

The complexity of communities and food webs are a crucial factor influencing species responses. A species is only as good as it can perform under the interaction of biotic and abiotic factors. Experiments with single species can reveal their potential to respond and adapt to different stressors. The harmful dinoflagellates alone, without any competition, would have, most likely, thrived under high nutrient conditions in all experiments. However, the ecological context is important for the determination of traits which are adapted and hence the response to a particular stressor (Van Doorslaer et al., 2010). For a better assessment of the relative success of HAB species, Wells *et al.* (2015) already suggested to include an artificial community and/or non-HAB species and thus direct interactions among phytoplankton in HAB laboratory studies. They also emphasised to consider multifactorial laboratory experiments with variations of multiple factors to understand responses and competitive outcomes of HAB and non-HAB species under more realistic climate change scenarios (Wells et al., 2015). In my experiments, especially competition and grazing played an important role for the bloom formation and demise of both harmful dinoflagellates, enhancing the importance to consider community interactions for HAB dynamics.

In all experiments, I found a strong interaction of diatoms and dinoflagellates, where especially diatoms were promoted by high nutrient conditions. Especially the result of Chapter 1 showed a strong temporal but also a strong spatial succession between the two groups. Diatoms dominated all communities after inoculation, especially at high nutrient concentrations, whereas dinoflagellate dominance occurred only at low nutrient concentrations after the diatom bloom began to decay. Similar to my results, natural diatom and dinoflagellate blooms have been found to be highly nutrient-dependent. In upwelling regions, diatoms appear during or shortly after the upwelling event. Dinoflagellates thrive after the diatom bloom when nutrient concentrations and mixing decreased and stratification increased again. Hence, upwelling systems show a strong temporal dependency of diatoms and dinoflagellates.

In Chapter 3, overall diatom growth was very strong and lead to a decrease of relative *L. polyedra* and dinoflagellate contributions to the total biomass, although absolute *L. polyedra* abundance even increased in one of the two communities. Results from experiments with both complex natural communities of the Southern Californian Coast (Chapter 3) indicated that initial community composition most likely shaped biomass and similarity responses to environmental changes. Initial community composition of both communities was relatively similar regarding group composition but differed strongly on the genus level. While one community (Point Dume) showed clear responses of increasing biomass and dissimilarity to nutrient pulses, the other community (Zuma Beach) responded more chaotic, without clear patterns. Differences in their responses could thus be attributed to differences in their initial community composition, as this was the strongest difference between both communities. This assumption is in agreement with findings from Eggers *et al.* (2014), who demonstrated that initial community composition had a greater influence on phytoplankton biomass than elevated CO2. In addition, Striebel *et al.* (2016) showed that community composition and biomass depended on the initial community composition in a temperature manipulation experiment with natural and artificially assembled communities.

Results from Chapter 3 indicate that initial community composition is a sensitive driver for community responses to environmental changes in nutrient concentrations. However, also in the case of community structure, trait-based approaches, linking community structure and

species diversity, can be used, as they provide a more mechanistic understanding why certain species are found under given environmental conditions (Litchman et al., 2010).

Another biotic factor that can be important for bloom dynamics, in general, is grazing. Five different kinds of grazers, which exhibit unique modes, have been shown to predate on HAB species: microbial pathogens, microzooplankton, mesozooplankton including copepods, benthic invertebrates, and fish (Wells et al., 2015). HAB species experience multiple and changing grazer attacks in all bloom phases and life cycle stages (Wells et al., 2015). In this study, grazing was only considered in Chapter 3, where the communities included micro- and mesozooplankton, such as ciliates, tintinnids and copepods. Microzooplankton is the main consumer of phytoplankton, as it takes up around 60-70% of the phytoplankton biomass (Turner, 2006). In Chapter 3, micro- and mesozooplankton grazer abundance increased with decreasing *L. polyedra* abundance, indicating that the increase of grazers could be explained by grazing on this dinoflagellate. Due to initial filtering, larger zooplankton, which in turn could have fed on micro- and mesozooplankton, was removed. The decrease of *L. polyedra* could have therefore been promoted due to the lack of higher trophic levels.

Conclusion

Overall bloom dynamics of *A. catenella* and *L. polyedra* are influenced by complex interactions of environmental abiotic and biotic factors, such as dissolved inorganic nutrients, competition between species and grazing. From my results I can draw the following conclusions:

- Both dinoflagellates are better competitors under low dissolved nutrient concentrations (Chapter 1 and 2) in simple artificial phytoplankton communities. In contrast, diatom competitiveness was better at high nutrient concentrations, where they became dominant very quickly. This study was the first approach to investigate this prevalent diatom and dinoflagellate interaction in a spatial and controllable context of a meta-ecosystem set-up.

- Dispersal is an important mechanism for organisms to migrate between habitats and thus thrive in habitats with favourable conditions. However, dispersal can also weaken

bloom formation under certain environmental conditions. Through the exclusion of dispersal, *A. catenella* became extremely dominant under low nutrient concentrations, whereas dominance was weaker when dispersal was allowed between all patches (Chapter 1). Hence, the flow of nutrients and organisms between habitats can have a fundamental influence on bloom development and persistence and should be considered in laboratory HAB experiments.

- Scaling should be considered carefully, as ecological processes can strongly vary between different spatial scales and influence HAB dynamics (Chapter 1 and 2).

- *L. polyedra* blooms are not promoted by nutrient pulses of dissolved nutrients (Chapter 3), and only little influenced by specific spatial or temporal inoculation along a nutrient gradient (Chapter 2). Even with an initial biomass advantage, *L. polyedra* was not able to maintain its prevalent position neither in an assembled community (Chapter 2) nor in a natural plankton community (Chapter 3).

- Traits diversity matters. *A. catenella* became dominant at lowest nutrient concentrations, whereas *L. polyedra* did not thrive at any time during the meta-ecosystem experiment (Chapter 1 and 2), indicating that both species must differ in their competitiveness e.g. resources, and thus in their traits. Functional traits are good predictors for variations in phytoplankton species responses and phytoplankton community structure (Edwards et al., 2013). Generalisations about phytoplankton groups can be helpful to understand general patterns, but understanding trait diversity might be a better indicator for harmful algal bloom dynamics.

- Community composition shapes responses to environmental changes. Results from Chapter 3 showed divergent patterns of the community development in two different communities through the addition of nutrient pulses, indicating the importance of the initial community composition. Communities are highly complex and underlay various food web dynamics, such as predation, predator avoidance and competition. The community composition is a result of their complex interactions among individual species and with abiotic environmental conditions. Thus, it is important to consider

food web interactions and community composition to understand community and HAB responses to environmental changes

This study showed, that dinoflagellate bloom dynamics are highly depended on overall community dynamics, including competition and grazing. Due to that, community dynamics and as such, species identities and trait diversity should always be considered to understand single species bloom dynamics.

In both, a more simplified and a complex community, diatom dominance was very strong and in most cases promoted by nutrients. Thus, the probably most prominent reason was, that diatoms generally have higher growth rates as well as higher carbon-specific nitrate uptake rates, than dinoflagellates, promoting their fast and strong biomass increase (Banse, 1982; Litchman et al., 2007). Hence, *L. polyedra* and *A. catenella* blooms are rather promoted by other factors than dissolved nutrients, at least as single factors only, as diatoms are better competitors for available dissolved nutrients. Other factors, for instance nutrient uptake through enhanced mixotrophic feeding, competitive release via the production of allelopathic substances or predator avoidance and nutrient uptake through vertical migration, might promote dinoflagellate blooms.

HAB dynamics are extremely complex and still not fully understood. However, this study provides another step towards a better understanding of blooming patterns of the two dinoflagellates *A. catenella a*nd *L. polyedra*, especially in the light of community dynamics and spatial propagation. For future HAB studies, spatial experimental applications, such as in meta-ecosystems, could provide a better understanding of ecological interactions of HAB forming species.

Summary

Harmful algal blooms (HABs) can lead to substantial ecological and economic losses due to their diverse negative effects on the ecosystem. Due to strong nutrient fluctuations, especially highly dynamic environments, such as upwelling systems, are prone to develop high phytoplankton biomass, including HABs. As these regions often play an important role for the fishing industry, they are particularly vulnerable to HAB events. It is therefore of general interest to identify factors initiating and promoting these blooms in order to implement or improve management strategies.
Over the last years some relationships of harmful algal blooms and environmental factors have been identified. However, many species-specific interactions with environmental factors are still unknown. Especially complex biotic interactions, such as competition and grazing in combination with other environmental factors remain unclear.

In this thesis, I therefore, investigated the effect of dispersal, community interactions and nutrients on the harmful dinoflagellates *Alexandrium catenella* and *Lingulodinium polyedra*. Both species regularly occur along the Southern Californian Bight (USA). However, while *A. catenella* is highly toxic and allelopathic, *L. polyedra* forms high-density blooms (so-called “red-tides”), which can lead to oxygen depletion in the water column.

In Chapter 1, I investigated the spatial propagation of the dinoflagellate *A. catenella* in a meta-ecosystem experiment, by inoculating *A. catenella* in different positions along a nutrient gradient. This experiment included competition with an artificially assembled community of four naturally co-occuring phytoplankton species. Results have shown, that *A. catenella* performed better under lower nutrient conditions. Also the inoculation position had a strong influence on their dynamics, especially when *A. catenella* was inoculated at lower nutrient conditions. A control experiment provided evidence, that dispersal had a major influence on *A. catenella* propagation, as it became highly dominant under lowest nutrient conditions, when dispersal was excluded.

The aim of the second Chapter was to test, whether *L. polyedra* blooms were influenced by the inoculation position and inoculation timing along a nutrient gradient. Here, the focus was on the spatial and temporal interactions in combination with the successional state of the community. *L. polyedra*

did not dominate the community, as diatoms were better competitors. However, *L. polyedra* still exhibited higher relative biovolume contributions at lower nutrient concentrations. Also *L. polyedra* was influenced by the inoculation position along the gradient, with stronger contributions at lower nutrient concentrations. The inoculation time, however, had only weak effects on its dynamics.

In Chapter 3, I studied bloom persistence and population dynamics during an autumn bloom of *L. polyedra* from two sites along the Southern Californian Bight. The *L. polyedra* bloom persistence was investigated in the context of competition with a naturally occurring community and the timing of nutrient additions. The initial high dominance of dinoflagellates, mostly *L. polyedra*, did not remain in the laboratory, neither with, nor without nutrient addition. Phytoplankton composition rapidly changed from a dinoflagellate dominated into a diatom-dominated community. In addition, the results indicated that initial community structure was important for the responses to the nutrient pulse, as it influenced biomass and dissimilarity differently.

This study provides better understanding of blooming patterns of the two dinoflagellates *A. catenella a*nd *L. polyedra*, especially in the light of community dynamics and spatial propagation. The results indicate, that both dinoflagellate blooms, *L. polyedra* and *A. catenella,* are promoted by other factors than dissolved nutrients alone Their competitive ability under low nutrient conditions might be promoted by a variety of strategies, such as nutrient storage, mixotrophic feeding, vertical migration or the production of allelopathic substances. Furthermore, this study showed, that species dynamics need to be investigated in more complex experiment setups, including biotic interactions such as competition, but also spatial aspects as these can fundamentally influence their performance.

Zusammenfassung

Schädliche Algenblüten (HABs; aus dem englischen „harmful algal blooms“) können aufgrund ihrer vielfältigen negativen Effekte auf das Ökosystem zu erheblichen ökologischen, aber auch wirtschaftlichen Verlusten führen. Aufgrund starker Nährstoffffluktuationen neigen besonders hochdynamische Systeme, wie beispielsweise Auftriebsgebiete dazu, HABs zu entwickeln. Da diese Regionen häufig eine wichtige Rolle für die Fischerei spielen, sind sie besonders anfällig für diese Algenblüten. Es ist daher von allgemeinem Interesse, die Faktoren zu identifizieren, die zu diesen Blüten führen, um Managementstrategien erstellen oder anpassen zu können.

In den letzten Jahren konnten bereits einige Zusammenhänge zwischen schädlichen Algenblüten und einigen Umweltfaktoren identifiziert werden. Jedoch sind viele Arten-abhängige Interaktionen mit Umweltfaktoren unklar. Insbesondere komplexe biotische Wechselwirkungen wie Konkurrenz und Fraß in Kombination mit anderen Umweltfaktoren sind weitestgehend unbekannt.

Daher untersuchte ich in dieser Arbeit die Auswirkungen von räumlicher Ausbreitung, Interaktionen in der Gemeinschaft sowie Nährstoffen auf die schädlichen Dinoflagellaten *Alexandrium catenella* und *Lingulodinium polyedra*. Beide Arten kommen regelmäßig in der Südkalifornischen Bucht (USA) vor. Während *A. catenella* toxisch und allelopathisch ist, bildet *L. polyedra* dichte Blüten (so genannte „red tides“), die zu Sauerstoffmangel im Wasser führen können.

In Kapitel 1 untersuchte ich die räumliche Ausbreitung des Dinoflagellats *A. catenella* in einem Meta-ecosystem-Experiment, indem ich *A. catenella* in verschiedenen Positionen entlang eines Nährstoffgradienten inokuliert hab. Dieses Experiment beinhaltete Konkurrenz mit einer künstlichen Gemeinschaft aus vier natürlich vorkommenden Phytoplanktonarten. Die Ergebnisse haben gezeigt, dass *A. catenella* unter niedrigeren Nährstoffbedingungen im Wettbewerb mit den anderen Arten der stärkere Konkurrent ist. Auch die Inokulations-position hatte einen starken Einfluss auf ihre Dynamik, insbesondere wenn *A. catenella* bei niedrigeren Nährstoffbedingungen hinzugegeben wurde. Der Kontrollversuch zeigte, dass die Ausbreitung in andere Habitate einen starken Einfluss auf die Dynamiken von *A. catenella* hatte, da sie unter den niedrigsten Nährstoffbedingungen stark dominierte, wenn eine Abwanderung in benachbarte Regionen nicht möglich war.

Das Ziel des zweiten Kapitels bestand darin, zu testen, ob *L. polyedra*-Blüten durch die Inokulations-position und den Zeitpunkt der Zugabe entlang eines Nährgradienten beeinflusst werden. Im Fokus lagen hierbei die räumlichen und zeitlichen Faktoren in Kombination mit dem Sukzessionszustand der Gemeinschaft. *L. polyedra* dominierte zu keinem Zeitpunkt die Gemeinschaft, da diese von Diatomeen dominiert wurden. *L. polyedra* zeigte jedoch bei niedrigeren Nährstoffkonzentrationen immer noch höhere relative Biovolumenbeiträge. Auch *L. polyedra* wurde durch die Inokulations-position entlang des Gradienten beeinflusst, wobei bei niedrigeren Nährstoffkonzentrationen ein größerer relativer Biovolumenanteil zu beobachten war. Der Zeitpunkt der *L. polyedra* Zugabe hatte jedoch nur geringe Auswirkungen auf Dynamiken von *L. polyedra.*

In Kapitel 3 untersuchte ich den Fortbestand sowie Populationsdynamik einer *L. polyedra* Herbstblüte von zwei Standorten entlang der Südkalifornischen Bucht. Die Blütedynamik wurde im Kontext einer natürlich-vorkommenden Gemeinschaft und mit unterschiedlichen Zeitpunkten der Nährstoffzugabe untersucht. Die anfänglich hohe Dominanz von Dinoflagellaten, meist *L. polyedra*, konnte weder mit noch ohne Nährstoffzugabe im Labor über längere Zeit bestehen. Die Zusammensetzung des Phytoplanktons änderte sich rasch von einer Dinoflagellaten zu einer Diatomeen-dominierten Gemeinschaft. Darüber hinaus zeigten die Ergebnisse, dass die anfängliche Gemeinschaftsstruktur für die Gemeinschaftsentwicklung in Reaktion auf den Nährstoffpuls wichtig war, da sie Biomasse und Gemeinschafts-Unähnlichkeit unterschiedlich beeinflusste.

Diese Arbeit hilft die Blühmuster der beiden Dinoflagellaten *A. catenella* und *L. polyedra*, insbesondere im Hinblick auf die Dynamik der Gemeinschaft und die räumliche Ausbreitung besser zu verstehen. Die Ergebnisse zeigen, dass beide Dinoflagellaten, (*L. polyedra* und *A. catenella*) durch andere Faktoren als gelöste Nährstoffkonzentrationen allein gefördert werden. Ihre Wettbewerbsfähigkeit unter niedrigen Nährstoffbedingungen kann durch verschiedene Strategien wie Nährstoffspeicherung, mixotrophe Nährstoffaufnahme, vertikale Migration oder die Produktion allelopathischer Substanzen beeinflusst werden. Darüber hinaus zeigte diese Studie, dass die das Verhalten von HABs in komplexeren Versuchsaufbauten untersucht werden muss, die sowohl biotische Interaktionen wie Konkurrenz, aber auch räumliche Aspekte berücksichtigt, da diese ihre Dynamiken grundlegend beeinflussen können.

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Danksagung

Besonders danken möchte ich Helmut Hillebrand für die Unterstützung bei meiner Dissertation, die Begutachtung dieser Arbeit und die ständigen Känguru-Anspielungen (VYVG AP).

Vielen Dank Steffi, für die Betreuung meiner Arbeit und die Möglichkeit im Rahmen dieser Arbeit nach Brasilien, Frankreich und natürlich in die USA reisen zu können. Das war eine wunderbare Erfahrung in meinem Leben für die ich dir sehr dankbar bin.

Ein großer Dank geht an Ulrike Feudel für ihre Bereitschaft diese Arbeit zu begutachten und die herzliche Zusammenarbeit. Ebenfalls danke ich Hans-Jürgen Brumsack für die Teilnahme als Prüfer am Promotionskolloquium.

Ein riesen Dank geht an die gesamt Planktology AG für die viele Unterstützung und die tolle gemeinsame Zeit. Besonders danken möchte ich: Andrea, Laura, Ola und Liisa für den vielen Spaß, die Problemlösungen jeglicher Art, die musikalische Untermalung und die ständige moralische Unterstützung. Lieben Dank geht auch an Doro für ihre statistische Hilfe. Danke Maren, das du mir so häufig mit Rat und Tat zur Seite standest.

Diese Arbeit wäre nicht möglich gewesen, hätten nicht so viele Leute mit angepackt. Daher auch nochmal einen riesen Dank an alle Helfer bei meinen Versuchen. Insbesondere Anna Moraldo und Lene Engelmann. Und natürlich vielen Dank an Heike Rickels für ihren unermütlichen Einsatz während meiner Versuche. Dank geht auch an Silke Ammermann für ihre Unterstützung.

I want to thank all members of the Caron lab, and Dave Caron in particular, for their great support during my stay at the USC in Los Angeles.

Ebenfalls möchte ich an dieser Stelle dem DAAD und der Prof. Dr. Bingel Stiftung für die finanzielle Unterstüzung für den Auslandsaufenthalt in den USA danken, sowie Carsten Lüter und Stefanie Lohmann für den anregenden Austauch.

Ich bin überaus dankbar für die moralische Unterstützung meiner Freunde und meiner Familie. Besonders Leon hat wahrscheinlich am meisten unter den Aufs und Abs dieser Arbeit gelitten. Daher geht ein riesen Dank für deine Liebe, dein Verständnis und auch für die vielen wissenschaftlichen Anregungen an dich, Leon.

Eidesstattliche Erklärungen

Hiermit versichere ich, dass ich die von mir vorgelegte Dissertation selbstständig verfasst und keine anderen als die angegebenen Hilfsmittel und Quellen genutzt habe. Alle Tabellen und Graphiken sowie alle wörtlich oder dem Sinn entnommenen Stellen sind von mir als solche gekennzeichnet.
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Anneke Purz

29.04.2020