


University of Groningen

and

Institute for Chemistry and Biology of the Marine Environment
(University of Oldenburg)

Bloom dynamics and propagation of the dinoflagellate *Alexandrium catenella*

Author:
Javier Alegria

Supervisor:
Dr. Stefanie Moorthi

Abstract

Harmful algal bloom (HAB) increase the area and concentration due to the ocean currents and the allelopathic interactions with the planktonic community. The present study investigates the population dynamics of *Alexandrium catenella* in a planktonic community along a nutrient gradient. To do so, a semicontinuous metacommunity experiment was performed using five interconnected flasks with a non-toxic planktonic community in each. *A. catenella* was added at two different nutrient concentrations (either highest or lowest nutrient concentration position) and dispersal between flasks was allowed. The results showed that dispersal is a suitable mechanism for *A. catenella* propagation and growth. *A. catenella* had a harmful allelopathic effect on the planktonic community after nutrients dropped, reducing the abundance of the other phytoplankton species only in the higher nutrient concentration positions of the gradient and regardless of the *A. catenella* concentration. This showed that harmful allelopathic effect can also depend on environmental conditions. Also, a theoretical model was used to determine how interrupted dispersal times affected the bloom dynamics, and the results showed that interrupted dispersal could favour bloom dispersal.

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1 INTRODUCTION

1.1 Harmful algal blooms

Phytoplankton are a diverse group of photosynthetic organisms at the base of the aquatic food web. It is responsible for generating half of the global primary production and can produce 50-80% of the total oxygen in the atmosphere. Furthermore, it absorbs up to half of the carbon dioxide released into the atmosphere, contributing to the mitigation of one cause of global warming (Falkowski et al. [2008], Field et al. [1998]).

Phytoplankton biomass and community composition are highly variable over time, with rapid increases in biomass when conditions are favorable. These increases are known as algal blooms, and even though some of them occur periodically, the exact time, intensity and location are unpredictable. About 3% of these blooms are categorized as harmful algal blooms (HAB) due to the potential negative impact they can cause, either directly, e.g. by oxygen depletion due to the decomposition of high algal biomass after the bloom demise, or directly, (e.g. *Akashiwo sanguinea* blooms have produced massive fish killings due to clogging the gills of the fishes(Amorim Reis-Filho et al. [2012])). Some HABs also produce toxins that can have a great negative impact on the ecosystem even at low cell concentrations. These toxins can damage potential consumers and even upper levels in the trophic chain due to bioaccumulation of the endotoxins. In fact, HABs toxins are closely linked with massive fish and shellfish killings (Lehane and Lewis [2000], Marie-Caroline Badjeck et al. [2010]), which have caused a great impact on fisheries and aquaculture (Anderson et al. [2000]). Moreover, these toxins can find their way through intoxicated species to human consumers, becoming a major threat to human health (Hallegraeff [2010]). Both industrial and health impact can cost up to 20.4 million US$ for a single bloom (Jin et al. [2008]), while on average economic losses through HABs sum up to 95 million US$ and 850 million US$ per year in the USA and Europe, respectively (Bernard et al. [2014]).

In the last few decades, the occurrence and intensity of HABs have increased dramatically, presumably due to the climate change and the increase of cultural eutrophication (Paerl et al. [2014], Hallegraeff [2010], Sellner et al. [2003], Van Dolah [2000]). Generally, HAB events are related to a wide list variety of abiotic factors, including dis-

solved nutrients, higher temperatures and pH. Thus, increasing temperatures can directly favour some HAB species (Xu et al. [2017]) as well as other associated factors, such as the ocean acidification (Wells et al. [2015]), stratification due to high temperatures (Berdalet et al. [2014]), increase of the ENSO occurrence (Rongo and van Woesik [2011]), etc. Yet, it has been pointed out that one of the main factors to understand the increasing HAB occurrence is cultural eutrophication (Wassmann et al. [2004], Anderson et al. [2002]), which increased exponentially after the popularization of chemical fertilizers during the 1950s (Smil [2004], Glibert et al. [2005]).

Nutrient requirements vary with taxonomic algal group; e.g. high nutrient conditions and pulses favor diatom blooms (Boynton et al. [1982], Malone et al. [1983]), while other algae such as the haptophyte *Prymnesium parvum*, are better competitors under nutrient limitation (Roelke et al. [2007]). This characteristics makes the bloom phenomena very wide and requires to be specific on the HAB species that is being investigated.

Dinoflagellates constitute 75–80% of the HAB species (Smayda and Reynolds [2003]). This group is known for being poor nutrient competitors when nutrients are plentiful and having low growth rates (Smayda [1997]). Therefore, most HAB species constitute a minor component of the natural phytoplankton community (Kudela et al. [2008]) and blooms are usually restricted to low nutrient conditions (Maguer et al. [2007]) or the increase of nitrogen/phosphate loading changing the nutrient ratios (Labry et al. [2008]) (e.g. an input of nitrogen can increase the nitrogen:silicate ratio (N:Si), limiting the growth of diatoms and facilitating other species that do not depend on silicate). When nutrients are plentiful, dinoflagellates usually have a minimum contribution to the total community and store nutrients until conditions are favourable for them (Dagenais-Bellefeuille and Morse [2013], Maguer et al. [2007], Smalley et al. [2003], Cembella et al. [1982]).

Dinoflagellates may also exhibit a heterotrophic feeding behavior in addition to photosynthetic carbon fixation, known as mixotrophy. In oligotrophic environments, potentially limiting nutrients are more concentrated in microbial prey than in the water column (Vadstein [2000]), providing mixotrophic organisims with a competitive advantage, as these organisms do not depend solely on dissolved nutrients, but can also use particulate nutrients; furthermore, they reduce potential competitor species by feeding (Reviewed in Jones [1994, 2000]). Mixotrophy is strongly related with the competing suc-

cess of dinoflagellates in low nutrient conditions (Burkholder et al. [2008], Glibert et al. [2009], Jeong et al. [2005]).

Some HAB species can also diminish the competitors and predators population by producing toxins and allelopathic exudates. Allelopathy is defined as any process involving secondary metabolites produced by plants, algae, bacteria and fungi that influence the growth and development of agricultural and biological systems (International Allelopathy Society [1996]). In the case of phytoplankton, allelopathic substances refer to the production of secondary metabolites that can negatively affect other components of the community such as competing species and potential consumers.

Allelopathic exudates are released into the surrounding medium and may have a great variety of effects on other phytoplankton species, such as growth inhibition (Yamasaki et al. [2009]), cell lysis (Ma et al. [2009]) and loss of motility (Tang and Gobler [2010]) among others. The effect on the target species depends on their cell size and concentration as well as on the duration of exposure (Tang and Gobler [2010], Tillmann et al. [2008], Lyczkowski and Karp-Boss [2014]). Therefore, allelochemicals give HAB species a competitive advantage (Tillmann et al. [2008], Tang and Gobler [2010], Poulson et al. [2010]), that may prolong the HAB and their impact on the ecosystem (Legrand et al. [2003]). Allelochemicals not only affect to competitors but have also been proven to affect consumer species (i.e. micro-zooplankton) (Jianing et al. [2016]). Despite the potential importance of these substances for bloom dynamics, the molecular composition and mechanisms involved are still poorly understood (Weissbach et al. [2010], Poulson et al. [2010]).

Toxicity in HABs is usually caused by endotoxins that are produced and stored inside the cell. When the toxic species are consumed these molecules may have a negative impact that could increase due to bioaccumulation and thus even affect to higher levels in the trophic chain that did not consume the phytoplankton directly(Lefebvre et al. [2016], Geraci et al. [1989]).

1.2 Harmful algal blooms in upwelling regions

HABs are especially recurrent in upwelling regions. In these systems, the wind blows parallel to the coast towards the equator, so Ekman transport in the boundary layer

directs surface waters offshore. The movement of great water masses away from the coast results in upwelling of cold and nutrient rich waters, overriding the nutrient limitation in the euphotic zone (Hood et al. [1992]). Thus, upwelling regions dynamics are linked to wind regimes, which vary through the year in upwelling-relaxation-downwelling cycles.

The California upwelling region is one of the biggest upwelling systems in the world. This region has a long history of amnesic shellfish poisoning (ASP) and paralytic shellfish poisoning (PSP) outbreaks, which need to be monitored monthly to prevent health and serious economic impact (see the Marine Biotoxin Annual Report: Langlois [2012], Bay [2010]) ASP is the results from the biotoxin domoic acid, which is produced by the diatom genus *Pseudo-niztschia* sp.. The presence of this toxin was confirmed in October 1991, and related to the intoxication of over 100 people in 1987, resulting in the death of three of them (Langlois [2006]). Despite an event like that has never happened again, concentrations of domoic acid exceeding the federal public health alert has been detected every year from 2000 to 2007 (Lewitus et al. [2012]) and in 2015 it was recorded the biggest bloom of *Pseudo-niztschia* sp..

PSP is caused by the endotoxin saxitoxin, which is produced by different species of dinoflagellates. Outbreaks of this toxins date back to the Native American tribes (Meyer et al. [1928]). This toxin has also caused a greater public health impact through history than ASP, as there has been 542 reported illnesses and 39 deaths caused by this toxin since 1927 (Price et al. [1991]). In recent years PSP activity has increased, affecting most notably the shellfish aquaculture industry in Santa Barbara and San Diego counties (Lewitus et al. [2012]). Saxitoxins are related to the dinoflagellate genera *Alexandrium*, *Gymnodinium* and *Pyrodinium*, but the main producer in the California upwelling region is *Alexandrium catenella* (taylor and trainer; michaela). This species is characterized by low density blooms (17cells ml^{-1}, Jester et al. [2009b]), but high toxicity (concentrations of 1cell ml^{-1} can produce health risk toxins concentration (Jester et al. [2009a])). *A. catenella* has a well documented allelochemical capacity (Arzul et al. [1999], Schmidt and Hansen [2001], Ribalet et al. [2007], Tillmann et al. [2008], Tillmann and Hansen [2009]), whose main effects are cell lysis and immobilization (Ma et al. [2009], Tillmann et al. [2008]).

A. catenella blooms generally occur during fall. In this season, HABs usually form offshore and the upwelling relaxation due to weaker winds allows the bloom to

move inshore (Lewitus et al. [2012]). Thus, transportation of blooms by dispersal and ocean water currents is an important factor to understand HAB dynamics. Ryan et al. [2009] studied Monterrey bloom dynamics and concluded that water transportation can drive dinoflagellate blooms, exacerbating the intensity and spreading the bloom depending on the conditions. Bialonski et al. [2016] indicated that water transportation may be determinant to understand HAB propagation and thus successional temporality between hydrologically interconnected regions.

This dependence on water movements indicate that bloom dynamics cannot be fully understood focusing the study on closed and isolated communities. Instead, the study on how plankton communities with a harmful species interact with each other on the bloom formation would be more accurate. These local communities that interact with each other are referred as metacommunities. The concept of metacommunity is receiving increasing attention to study how interaction between communities affect to species richness (Cadotte [2006]), colonization of new communities by species (Louette and Luc [2005], Logue et al. [2011]), extinction and rescue effects (Hunt and Bonsall [2009]), etc. However, little attention has been paid to the dynamics of harmful phytoplankton species on a metacommunity.

1.3 Aims and hypothesis of the study

This project studies the spatial dynamics of *A. catenella* in a non-toxic phytoplankton community consisting of three different species in a metacommunity system, i.e. five interconnected flasks with nutrient gradient. Dispersal between flasks was allowed only during two minutes every day. *A. catenella* was inoculated at the end of the metacommunity, either on the low or high nutrient concentration flask. An additional treatment without *A. catenella* served as the control. All treatments were set up with or without the presence of a micro-zooplankton consumer (*Brachionus plicatilis*). The aim of this setup is to investigate the propagation and competitive interactions of *A. catenella* with other phytoplankton along the nutrient gradient in dependence of its inoculation position (i.e. local nutrient conditions). Furthermore, the effect of a potential consumer on these dynamics, which is known to be negatively affected by allelochemicals produced by the *A. catenella* strain used in this experiment.

In addition, a theoretical model was used to determine the potential effects of the pulsed dispersal on the system dynamics. To do so, the metacommunity experiment was reproduced based on the model of Chakraborty and Feudel [2014] and the biomass of each two phytoplankton species (one toxic and another non-toxic) was calculated at equilibrium increasing the time of dispersal from 0 hours a day (no dispersal) to 24 hours a day (continuous dispersal) keeping a constant absolute dispersal.

The following hypotheses were investigated at two scales based on the experiment results: at a regional scale for different consumer and inoculation treatment across all flasks of a metacommunity and at a local scale, comparing response variables through the gradient in each treatment with the control. An additional hypothesis was also tested with the theoretical model.

Regional scale:

Hypothesis H1: A. catenella relative contribution to the phytoplankton community will be higher when inoculated at low nutrient concentration because dinoflagellates are better competitors when nutrients are not plentiful.

Hypothesis H2: A. catenella decreases the total BV of the non-toxic algae and modifies the phytoplankton community structure because the susceptibility towards allelopathy is species-specific (Tillmann et al. [2008]).

Hypothesis H3: A. catenella decreases *B. plicatilis* abundance due to allelochemical effects; this effect increases with relative abundance of *A. catenella*.

Hypothesis H4: B. plicatilis decreases total algal BV and *A. catenella* relaive abundance due to grazing pressure and alters the community structure, depending on the preferred species by the grazer.

At a local scale:

Hypothesis H5: The non-toxic community total BV will be distributed in a gradient, increasing with higher nutrient concentrations.

Hypothesis H6: A. catenella disperses through the experimental units, reaching the highest contribution at or close to the inoculation position (bloom expansion). The relative abundance of *A. catenella* is higher when it is inoculated at low nutrient positions,

because dinoflagellates are better competitors when nutrients are not plentiful.

Hypothesis H7: A. catenella decreases *B. plicatilis* abundance due to allelochemical effects; this effect increases with *A. catenella* relative abundance.

Hypothesis H8: A. catenella decreases the total algal BV and modifies the community structure. This effect increases with relative abundance of *A. catenella*.

Hypothesis H9: B. plicatilis decreases the total algal BV and *A. catenella* relative abundance and alters the community structure. The grazing preassure of *B. plicatilis* also hinders *A. catenella* dispersal through the gradient.

Model hypothesis:

Hypothesis H10: The toxic species will dominate when there is low dispersal time, because that allows the toxic species to increase the concentration on each community and thus increase the allelopathic effect outcompeting the non-toxic species.

2 MATERIALS AND METHODS

2.1 Algae cultures and methods of growth.

The HAB species used in the experiment was *Alexandrium catenella*. The non-toxic phytoplankton community consisted of *Leptocylindrus* sp. (diatom), *Prorocentrum micans* (dinoflagellate) and *Rhodomonas abbreviate* (cryptophyte). All phytoplankton cultures, including *Alexandrium catenella*, were isolated from the coast of Southern California (Caron Laboratory, USC, Los Angeles) and grown in f/2 medium (Guillard and Ryther [1962]; Appendix 1).

The grazer used in the experiment was *Brachionus plicatilis*. This species was derived from the Systematic and Evolution Biology laboratory (Prof, Bininda-Emonds, Oldenburg University, Germany) and grown f/2 medium in non-axenic conditions with the chlorophyte *Tetraselmis* sp. as a food source.

Stock cultures were grown in a climate chamber at 18 °C with a 12:12 h light:dark cycle, illuminated by cool-white fluorescence lights with an intensity of 60 μmol photons m^{-2} s^{-1}.

2.2 Experimental design.

To test the population dynamics of *A. catenella* in a phytoplankton a community along a nutrient gradient, a semi-continuous metacommunity experiment was conducted. Each community unit consisted of five 100 ml interconnected metacommunity flasks, each of which contained 70 ml of modified f/2 medium following the Redfield-Brezezinski ratio of Si:N:P = 15:16:1 (Redfield [1934], Brezezinski [1985]). A nutrient gradient was established along each metacommunity unit by increasing the silicate, nitrogen and phosphate concentrations from Si:N:P = 17.65μmol L^{-1}:16.55μmol L^{-1}:1.1μmol L^{-1} in position 1 to Si:N:P = 17.65μmol L^{-1}:16.55μmol L^{-1}:1.1μmol L^{-1} in position 5 (table 1). All species of the non-toxic community were inoculated in all flasks with the same biovolume (BV), approximating in total 4% of the maximum BV at the stationary phase (98492822.99 μm^3). BV of each species was estimated using volumetric formulae (Hillebrand et al. [1999]; methodology in Appendix 2).

Table 1 Initial nutrient concentration of the metacommunity flasks.

	Nitrogen (μmol L^{-1})	**Silicate(μmol L^{-1})**	**Phosphate(μmol L^{-1})**
Flask 1	17.65	16.55	1.10
Flask 2	53.23	49.91	3.33
Flask 3	88.83	83.27	5.55
Flask 4	124.41	116.63	7.78
Flask 5	160	150	10

The treatments consisted of two different inoculation positions (position 1 and position 5) for *A. catenella* at the same BV as the other phytoplankton species (1313237.64 μm^3; $\sim$155cells ml^{-1}). One extra treatment without *A. catenella* was used as a control. One set of these three treatments was setup without *B. plicatilis*: *A. catenella* addition in position 1 (NBA1), *A. catenella* addition in position 5 (NBA5) and control (NBNA). Additionally, another set consisting of these three treatments was set up, adding 25 individuals of *B. plicatilis* to each flask. After six days of experiment, 50 extra individuals were added to each flask because *B. plicatilis* got extinct after only three days of experiment. The treatments with *B. plicatilis* were: *A. catenella* addition in position 1 (BA1), *A. catenella* addition in position 5 (BA5) and control (BNA) (Fig. 1). All treatments were run in triplicate.

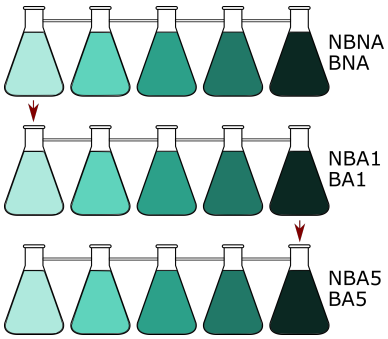

Figure 1 Schematic representation of the set-up. Red arrows point where the *A. catenella* is inoculated on each treatment (NBNA=control with *B. plicatilis* addition, BNA=control without *B. plicatilis* addition; NBA1=*A. catenella* addition in position 1 without *B. plicatilis* addition, BA1=*A. catenella* addition in position 1 with *B. plicatilis* addition; NBA5=*A. catenella* addition in position 5 without *B. plicatilis* addition, BA5=*A. catenella* addition in position 5 with *B. plicatilis* addition).

All treatments and control sets were incubated in the climate chamber under the same conditions previously described on top of a shaking table to avoid phytoplankton sinking. Every day, the connections between all flasks were opened for two minutes to allow dispersal between flasks. Every third day, 8.25ml subsamples were taken under the clean bench from all metacommunity flasks to measure absorbance with a fluorometer as

a proxy for chlorophyll a (*chl a*), after which 3.25ml were fixed in lugol for microscopic counts and the remaining 5ml were used to measure dissolved nutrient concentrations of phosphate, silicate and nitrate. Dissolved nutrient samples were filtered (0.2 μm mesh size), diluted with 5ml of ultrapure water, stored at 4°C and measured within the next 24 hours. The number of *B. plicatilis* cells was estimated by counting 20ml of each flask using a stereomicroscope, after which the volume was put back in the corresponding flask. After each sampling, 8.25ml of the fresh medium of the corresponding nutrient concentration was filled back into each metacommunity flask.

Chl a fluorescence enabled to follow algal biomass dynamics directly in the time course of the experiment. In the light of these results, four sampling days were chosen for microscopic counts and to calculate the BV of each phytoplankton species. For that, a minimum of 400 cells of each species from a 0.5-1ml lugol subsample were counted under an inverted microscope (Leica DM IL).

2.3 Contamination in BA1

In BA1 the *Tetraselmis* sp. associated to *B. plicatilis* contaminated all replicates and even dominated in some of the positions (data not shown). This was consistent with all days counted under the inverted microscope. For this reason, BA1 had to be excluded from the statistical analysis.

2.4 Data analysis

The regional analysis explored the differences between treatments (inoculation position of *A. catenella*, presence of *B. plicatilis*) on the total algal BV, the relative contribution of *A. catenella* to the total algal BV (due to grazing or nutrient conditions) and the allelophatic impact on the plankton community across all metacommunity flasks. The allelopathic impact was analysed in three different response variables: the total BV of the non-toxic community, the relative contribution of each species to it and the number of *B. plicatilis* cells. The averages of all sampling days were pooled for these for each replicate of these response variables and analysed by a one-way analysis of variances (ANOVA, p=0.05). In case of significant treatment effects, a Tukey-Kramer post hoc test

was performed.

The local analysis explored the total algal BV and the dispersal of *A. catenella* along the nutrient gradient in dependence of the inoculation position and *B. plicatilis* abundance. The *B. plicatilis* could not be analysed statistically due to the small sample size; therefore, results were described directly from the raw data and figures.

Total BV, relative abundance of *A. catenella* and nutrient concentration were tested by a linear mixed effect model (Bates et al. [2014]) including the fixed-factors treatment (five levels: NBNA, NBA1, NBA5, BNA, BA5) and the nutrient flask position (five levels: position 1, 2, 3, 4 and 5; from low nutrient concentration (position 1) to high nutrient concentration (position 5)), and their interaction was used to explain the variation of the effects depending on the initial input position of *A. catenella*. The number of unit (each full set of five interconnected flasks) was considered as the random-factor in the model. The model was analysed with an ANOVA type II (Weisberg and Sanford [2011]) with a level of significance of 0.05, although p=0.1 was also considered as marginally significant. When results were significant, the differences between treatments or interaction between treatments and position were analysed by calculating the 95% percentile bootstrap confidence interval (2000 simulations) using as a baseline the treatment with more potential significant differences.

All the analysis were performed using R version 3.3.1 (R Core Team [2016]).

2.5 Model description

The model represents a metacommunity formed by 5 different communities connected via dispersal (Fig. 2A). On each community the model describes the interaction between a toxic phytoplankton population ($P_{T_n}(t)$), a non-toxic phytoplankton population ($P_{N_n}(t)$) feeding and competing for one nutrient ($N_n(t)$) and a grazing zooplankton population ($Z_n(t)$) that feeds on both phytoplankton populations (Fig. 2B). Here, the units of $N_n(t)$, $P_{N_n}(t)$, $P_{T_n}(t)$,and $Z_n(t)$ are in grams of carbon per cubic meter. The interplay of the different species is determined by the growth of phytoplankton upon the nutrient, growth of zooplankton due to grazing of phytoplankton, mortality of phytoplankton and zooplankton by sinking and allelopathy, and the perodic introduction of nutrients every third day as well as recycling by bacteria which are not explicitly taken into account

in the model. These processes are described mathematically by the following equations equations (based on Chakraborty and Feudel [2014] and Chakraborty, in preparation) and performed by a fixed set of parameter values (table 2):

$$\frac{dN_n}{dt} = -\sum f_N(N_n) f_g(P_{N_n}, P_{T_n}) P_i + \sum r P_i + \sum \beta f_{Z_i}(P_N, P_T) Z + \gamma dZ + f_h(P_T) Z + \Delta f(N_n, N_{n+1}, N_{n-1}) \tag{1}$$

$$\frac{dP_{N_n}}{dt} = \alpha_{N_N} f_N(N_n) f_g(P_{N_n}, P_{T_n}) P_{N_n} - r P_{N_n} - f_{Z_N}(P_{N_n}, P_{T_n}) Z - (s+k) P_{N_n} + \Delta f(P_{N_n}, P_{N_{n+1}}, P_{N_{n-1}}) - f_{h_{P_{N_n}}}(P_{T_n}) \tag{2}$$

$$\frac{dP_{T_n}}{dt} = \alpha_{N_T} f_N(N_n) f_g(P_{N_n}, P_{T_n}) P_{T_n} - r P_{T_n} - f_{Z_T}(P_{N_n}, P_{T_n}) Z - (s+k) P_{T_n} + \Delta f(P_{T_n}, P_{T_{n+1}}, P_{T_{n-1}}) \tag{3}$$

$$\frac{dZ_n}{dt} = \alpha_{Z_T} f_{Z_N}(P_{N_n}, P_{T_n}) Z_n + \alpha_{Z_N} f_{Z_T}(P_{N_n}, P_{T_n}) Z - dZ_n - f_h(P_{T_n}) Z_n + \Delta f(Z_n, Z_{n+1}, Z_{n-1}) \tag{4}$$

Where n represents each community in Fig. 2A. The nutrient uptake is represented by $f_N(N)$:

$$f_N = \frac{N_n}{e + N_n} \tag{5}$$

Where e is the half saturation constant. Growth limitation of phytoplankton is described by the function:

$$f_g(P_{N_n}, P_{T_n}) = \frac{a}{b + cP_{N_n} + cP_{T_n}} \tag{6}$$

This function describes the growth limitation due to light attenuation by the water (b) and shelf-shading of the phytoplankton (c). a/b is the maximum nutrient uptake

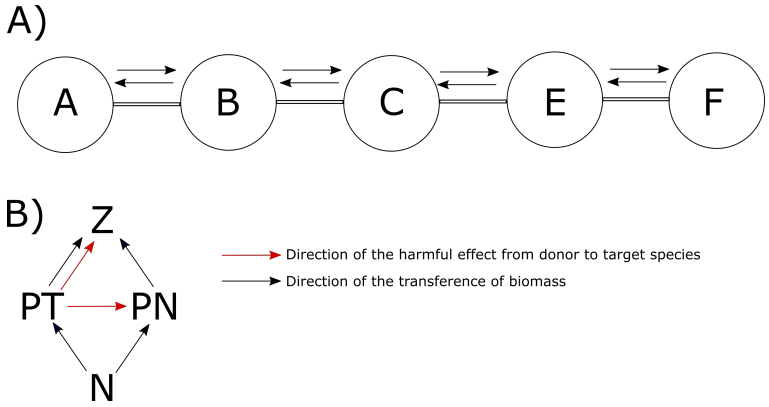

Figure 2 schematic representation of A) the metacommunity with five communities interconected by dispersal (direction of dispersal pointed by arrows) and B) representation of the main transferences of biomass in the system (black arrows) and the harmful effect of the toxic phytoplankton on zooplankton (red arrow)

rate by phytoplankton. The proportion of up taken nutrients that ultimately transforms into phytoplankton biomass is defined by α_{N_N} and α_{N_T} for non-toxic and non-toxic phytoplankton respectively, being $\alpha_{N_N} > \alpha_{N_T}$.

The function $f_{Z_i}(PN_n, PT_n)$ describes the feeding rate of zooplankton on the two phytoplankton populations (Ryabchenko et al. [1997]):

$$f_{Z_i}(PN_n, PT_n) = \frac{\lambda \phi_i^2 Z}{\mu + \phi_i P_{i_n}^2 + \phi_j P_{j_n}^2} \tag{7}$$

Where λ is the maximum zooplankton feeding rate, μ is the zooplankton grazing half-saturation constant, ϕ_N and ϕ_T is the grazing preference for the phytoplankton population for non-toxic and toxic phytoplankton respectively. Grazing preference rages from 0 to 1 and always $\phi_{N_N} + \phi_{N_T} = 1$ (Solé et al. [2006]). In this case, $\phi_{N_N} > \phi_{N_T}$, which provides the toxic phytoplankton a competitive advantage over the non-toxic phytoplankton (a trade-off for the lower growth efficiency of the toxic phytoplankton). The function $f_{h_Z}(P_{T_n})$ describes the mortality of the zooplankton due to the allelopathy of the toxic phytoplankton (Chakraborty, in preparation):

$$f_{h_Z}(P_{T_n}) = \frac{\theta_Z P_{T_n}^2}{\vartheta_Z^2 + P_{T_n}^2} \tag{8}$$

Where θ_Z represents the intensity of the allelopathic effect and ϑ_Z represents the half saturation constant for allelopathy. The allelopathic effect on the non-toxic phytoplankton is described by the function:

$$f_{h_{P_{N_n}}}(P_{T_n}) = \frac{\theta_{P_N} P_{T_n}^2}{\vartheta_{P_N}^2 + P_{T_n}^2} \tag{9}$$

Where $\theta_{P_{N_n}}$ represents the intensity of the allelopathic effect and $\vartheta_{P_{N_n}}$ represents the half saturation constant for allelopathy.

The parameter r represent the loss of phytoplankton biomass for respiration. γ represents the mortality rate of the zooplankton. β and γ represent the recycling rates of bacteria for the grazing rate and zooplankton death rate respectively.

The function $\Delta f(i_n, i_{n+1}, i_{n-1})$ represents the dispersal:

$$\Delta f(i_n, i_{n+1}, i_{n-1}) = \frac{D}{\Delta x^2}(i_n + i_{n+1} + i_{n-1}) \tag{10}$$

D represents the dispersal rate between communities (n) for nutrients, zooplankton and the two phytoplankton populations (i); x represents the distance between communities.

This model aims to investigate the effect on the equilibrium of P_N and P_T by gradually increasing dispersal times between communities keeping a constant absolute dispersal. To keep a constant absolute dispersal, the following equivalence was used:

$$D_2 = \frac{T_1^3 D_1}{T_2^3} \tag{11}$$

Where D_1 is the dispersal rate when dispersal is allowed for T_1 (hours day$^-$1) on each day (table 2) and D_2 changes accordingly with increasing T_2 (hours day$^-$1) raging from 0 to 24 (hours day^{-1}). A nutrient gradient was estabished along the metacommunity (Fig 2A; initial values: N_{o_1}, 0.2 g Cm$^-$3; N_{o_2}, 0.4 g Cm$^-$3; N_{o_3}, 0.6 g Cm^{-3};N_{o_4}, 0.8 g Cm$^-$3 and N_{o_5}, 1 g Cm^{-3}). The non-toxic phytoplankton (P_N) was established in all communities at initial concentration of 0.01 g Cm^{-3} and the zooplankton (Z) at 0.1 g Cm^{-3}. The toxic phytoplankton (P_T) only was stablished in either the lowest nutrient concentration community (0.2 g Cm^{-3}) or the highest nutrient concentration community (1 g Cm^{-3}) (Fig. 2A) at the same concentration as P_N (0.01 g Cm^{-3}.) The toxic phytoplankton dispersed through the metacommunity when dispersal was allowed (T_2). Every third day of the simulations there is a dilution of 10% for N, P_N, P_T and Z and the addition of 10% of the initial nutrient concentration corresponding to each community.

Table 2 Parameter definitions, default values and ranges. The ranges are based on values used in a variety of other models and given by Edwards [2001] and Chakraborty and Feudel [2014]

Paramenter	*Symbol*	*Default value*	*Reported range*
a/b gives maximum P growth rate	a	$0.2\text{m}^{-1}\text{day}^{-1}$	0.07-0.28
Light attenuation by water	b	0.2m^{-1}	0.04-0.2
Phytoplankton self-shading coefficient	c	0.4 m^2 $(\text{g C})^{-1}$	0.3-1.2
Mortality rate of Z	d	0.12 day^{-1}	0.015-0.15
Half-saturation constant for N uptake	e	0.03 g C m^{-3}	0.02-0.15
Phytoplankton respiration rate	r	0.15 day^{-1}	0.05-0.15
Z growth efficiency due to P_N	α_N	0.25	0.2-0.5
Z growth efficiency due to P_T	α_T	0.2	0.2-0.5
Z excretion fraction	β	0.33	0.25-0.8
Regeneration of Z predation excretion	γ	0.5	0.5-0.9
Maximum Z grazing rate	λ	0.6 day^{-1}	0.6-1.4
Z grazing half saturation	μ	0.02 g C m^{-3}	0.02-1.0
Conversion rate of nutrient into P_N	α_{Z_N}	0.25	0.2-0.5
Conversion rate of nutrient into P_T	α_{Z_T}	0.2	0.2-0.5
Z preference for P_N	ϕ_N	0.6	0-1
Z preference for P_T	ϕ_T	0.4	0-1
Strength of allelopathic effect on Z	θ_Z	0.08 day^{-1}	-
Half-saturation constant for allelopathy on Z	ϑ_Z	0.02 g C m^{-3}	-
Strength of allelopathic effect on P_N	θ_{P_N}	0.15 day^{-1}	-
Half-saturation constant for allelopathy on P_N	ϑ_{P_N}	0.04 g C m^{-3}	-
Dispersal rate when dispersal time is T_1	D_1	0.02 m^2 day hours^{-1}	-
Dispersal time when dispersal rate is D_1	T_1	0.011 hours $\text{day}^{-}1$	-
Dispersal rate when dispersal time is T_2	D_2	variable m^2 day hours^{-1}	-
Dispersal time when dispersal rate is D_2	T_2	variable hours $\text{day}^{-}1$	0-1
Distance between communities	x	1 m	-

3 RESULTS

The *chl a* measurements provided an approximation on the total biomass on each treatment in the course of the experiment (Fig. 3A). From day 3 to day 6 *chl a* increased exponentially in all treatments, with no apparent differences between treatments. From day 6 to day 12 *chl a* decreased in the treatments that included *B. plicatilis* (BA5 and BNA) as *B. plicatilis* increased (Fig. 3E), while no stationary phase was observed. In the same time span NBNA, NBA1 and NBA5 entered a stationary phase that ended when nitrate and silicate became limiting on days 12 and 15 respectively. On day 15, the *chl a* in NBNA, NBA1 and NBA5 decreased 70% on average, recording similar values as BA5 and BNA. From this day on, all treatments showed similar low values until the end of the experiment.

Under the light of these results, four days were chosen for microscopic counts to calculate the BV of each species in the metacommunity flasks: day 6 (exponential phase), day 12 (stationary phase), day 15 (end of stationary phase) and day 24 (end of the experiment).

3.1 Regional dynamics

A. catenella increased in cell concentration starting from ∼30cells ml^{-1} to a maximum of ∼155cells ml^{-1} ($\pm$SE=75.74) on NBA5 on day 15 (Fig. 3B). The exponential phase took place in the first 6 days of the experiment and after that, the concentration stabilized. The relative contribution and concentration of *A. catenella* was not significantly affected by the nutrient concentration in the input position, rejecting *H1* (table 3; Fig. 3C). Yet, the relative contribution of *A. catenella* was always lower in NBA1 than in NBA5 and BA5; especially on day 15 (end of stationary phase) and day 24 (end of experiment). The highest relative contribution was observed in NBA5 (5.69% $\pm$SE 1.67) on day 15, after the decrease in total biomass and nutrients (Fig. 3A, D, F, G, H). On that day the differences on *A. catenella* relative abundance between NBA1 and BA5 and NBA reached a maximum value.

The total BV results matched the observations of the *chl a*, also showing a general increase from day 6 to day 12, and a decrease from day 12 to day 15 remaining

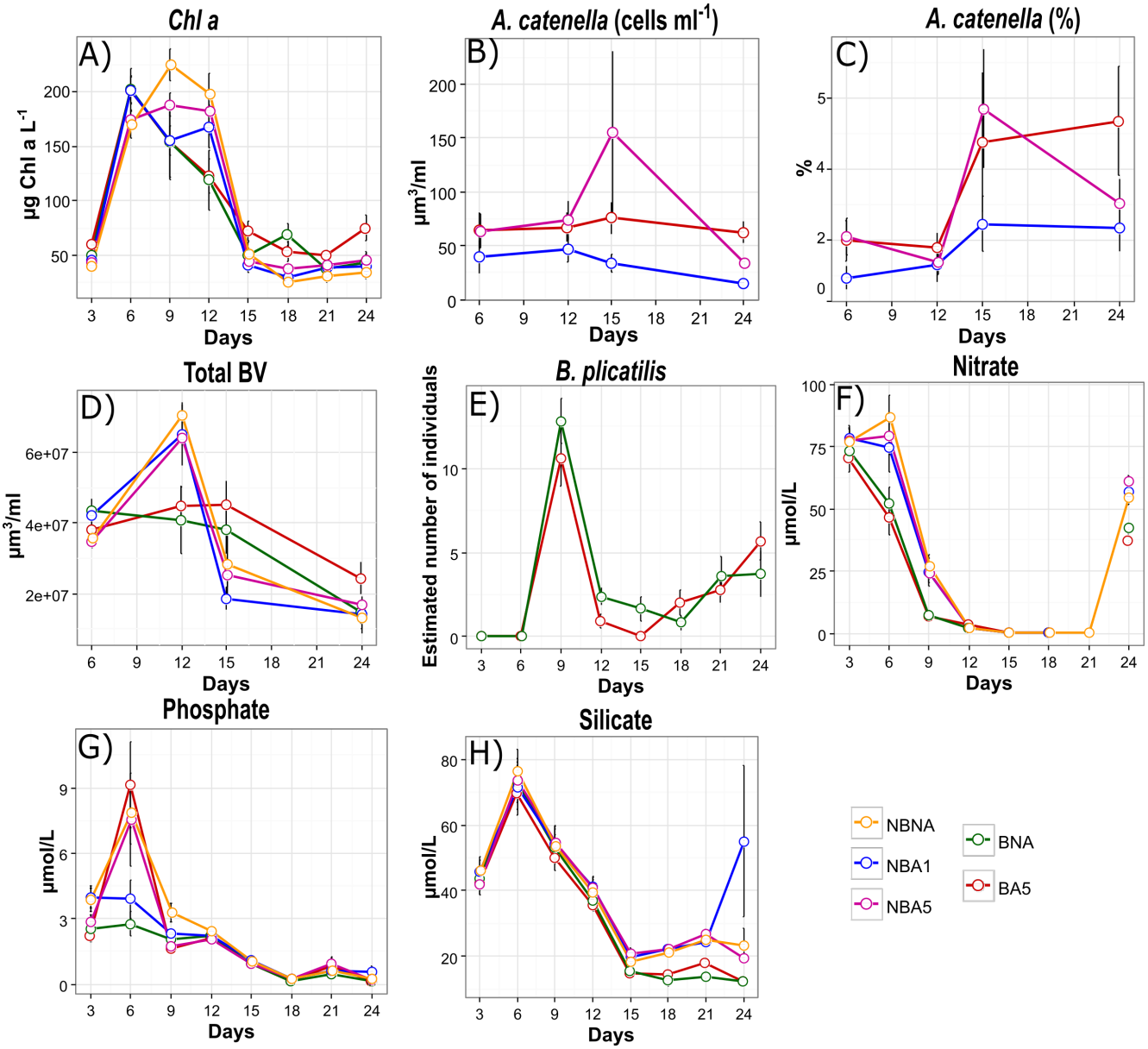

Figure 3 Mean values$^{+}_{-}$SE on each day for A)*Chl a*, B)*A. catenella* biovolume concentration (μ m^3/ml), C) *A. catenella* relative contribution (%), D)total algal BV (μ m^3/ml), E)*B. plicatilis* individuals, F) nitrate (μmol/L), G) phosphate (μmol/L), H) silicate (μmol/L).

with constant values until day 24 (Fig. 3D). *A. catenella* did not have any significant negative effect on the total BV nor altered the community structure, rejecting *H2* (table 3; Fig 3D and 4).

The treatment with *A. catenella* (BA5) presented similar *B. plicatilis* population and trends to the control treatment (BNA) (Fig. 3E) (rejecting with *H3*). *B. plicatilis* was less abundant in BA5 than in BNA, especially on day 15, when *B. plicatilis* was undetectable in BA5 while it was observed in BNA. After day 15 *B. plicatilis* abundance increased in both BA5 and BNA, showing no clear differences between treatments.

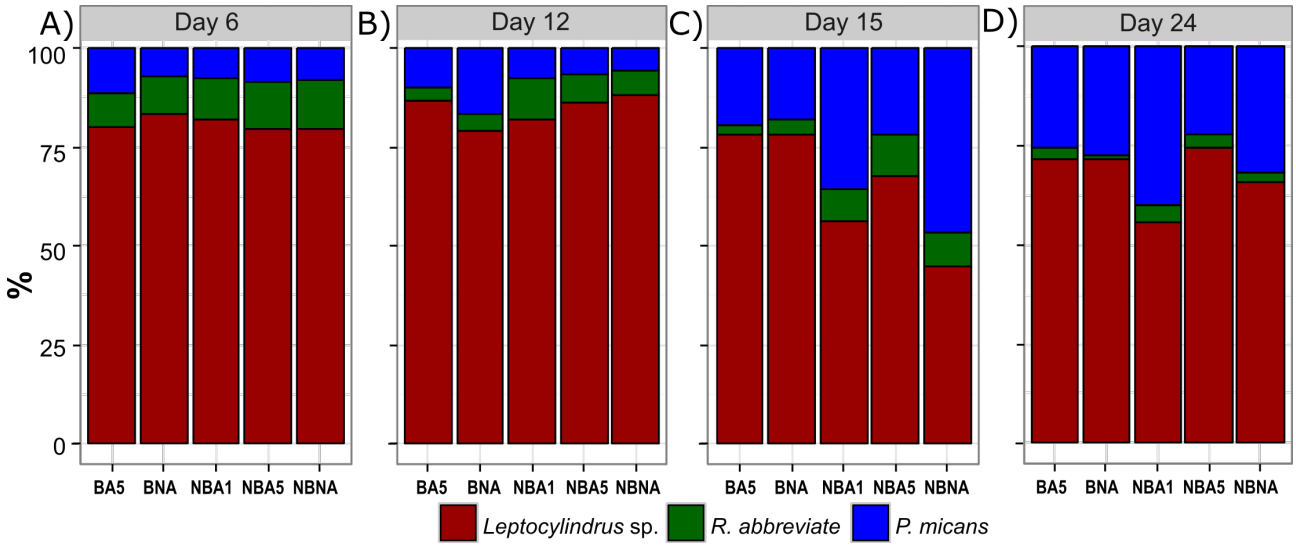

Figure 4 Mean relative abundance (%) on each treatment of *Leptocylindrus* sp., *Prorocentrum micans* and *Rhodomonas abbreviate* on A) day 6, B) day 12, C)day 15, D) day 24.

B. plicatilis did not reduce significantly the total BV (nor *A. catenella* relative abundance) in any of the days (rejects *H4*), despite the lower total BV in BA1 and BNA compared to the rest of the treatments on day 12 (table 3; Fig. 3 D). *B. plicatilis* altered significantly the community structure reducing the relative contribution of *R. abbreviata*, supporting *H4* on this respect. (table 3; Fig. 4).

Table 3 One factor Anova and Tukey-Kramer post hoc test analysing the overall differences of the total algal BV and the relative contributions of *A. catenella*, *Leptocylindrus* sp., *P. micans* and *R. abbreviate*

	df	*Fvalue*	*p-value*
A. catenella (%)	2	1.05	0.405
Total BV	4	0.45	0.765
Leptocylindrus sp. (%)	4	1.66	0.235
P. micans (%)	4	0.97	0.461
R. abbreviate (%)	4	17.190	<0.001***
Tukey-Kramer post hoc test			
R. abbreviate (%)			
	BNA-BA5	0.348	
	NBNA-BA5	0.001**	
	NBA5-BA5	<0.001****	
	NBA1-BA5	<0.001****	
	NBNA-BNA	0.020*	
	NBA5-BNA	0.011*	
	NBA1-BNA	0.007**	
	NBA5-NBNA	0.9932075	
	NBA1-NBNA	0.9646847	
	NBA1-NBA5	0.9992423	

Table 4 Concentration of *A. catenella* (cells ml^{-1}) in each nutrient position each day.

		Day 12		Day 15	
Nut. pos.	**Treatment**	**cells ml^{-1}**	**SE**	**cells ml^{-1}**	**SE**
1	BA5	16.67	12.67	29.33	16.01
2	BA5	28.67	11.79	52.67	22.93
3	BA5	51.33	15.76	60.00	20.00
4	BA5	113.33	26.77	111.00	63.00
5	BA5	125.33	18.77	137.33	18.56
1	NBA1	85.33	46.80	58.00	27.30
2	NBA1	58.00	22.48	44.00	20.82
3	NBA1	34.67	17.14	23.33	12.13
4	NBA1	28.67	9.96	20.00	8.00
5	NBA1	16.00	2.00	16.67	3.53
1	NBA5	18.00	4.00	30.00	3.06
2	NBA5	21.33	8.82	46.67	6.36
3	NBA5	39.33	16.01	73.33	20.80
4	NBA5	88.67	26.39	107.00	19.00
5	NBA5	182.00	9.24	502.00	308.95

3.2 Local dynamics

For the local analyses, only the results for day 12 and 15 are presented. Days 6 and 24 did not show any meaningful results (Appendix 3).

The nutrient gradient for the phosphate and silicate was present on both analysed days (day 12 and 15), however, the gradient for nitrate was not present. The concentration of all nutrients decreased from the initial values, meaning that the high nutrient concentration positions had lower nutrient concentrations than the low nutrient concentration position at the begining of the experiment (table 1, Fig. 5E, F, G and 6E, F, G). The total algal BV increased with increasing nutrient concentrations on days 12 (all treatments except for NBA5) and 15 (all treatments), supporting *H5* (Fig. 5A, D, E, F and Fig. 6A, D, E, F).

A. catenella propagated through the metacommunities in a decreasing gradient from its input position in all treatments, in agreement to *H6* (Fig. 5B, 6B). The initial concentration of ∼155cells ml^{-1} in the input position decreased in all treatments except for NBA5, which showed a constant increase through the days. The neighbouring positions to the inoculation position increased their concentration approximating initial concentration of the inoculation (table 4).

Treatment and position (i.e. nutrient concentration) significantly and interac-

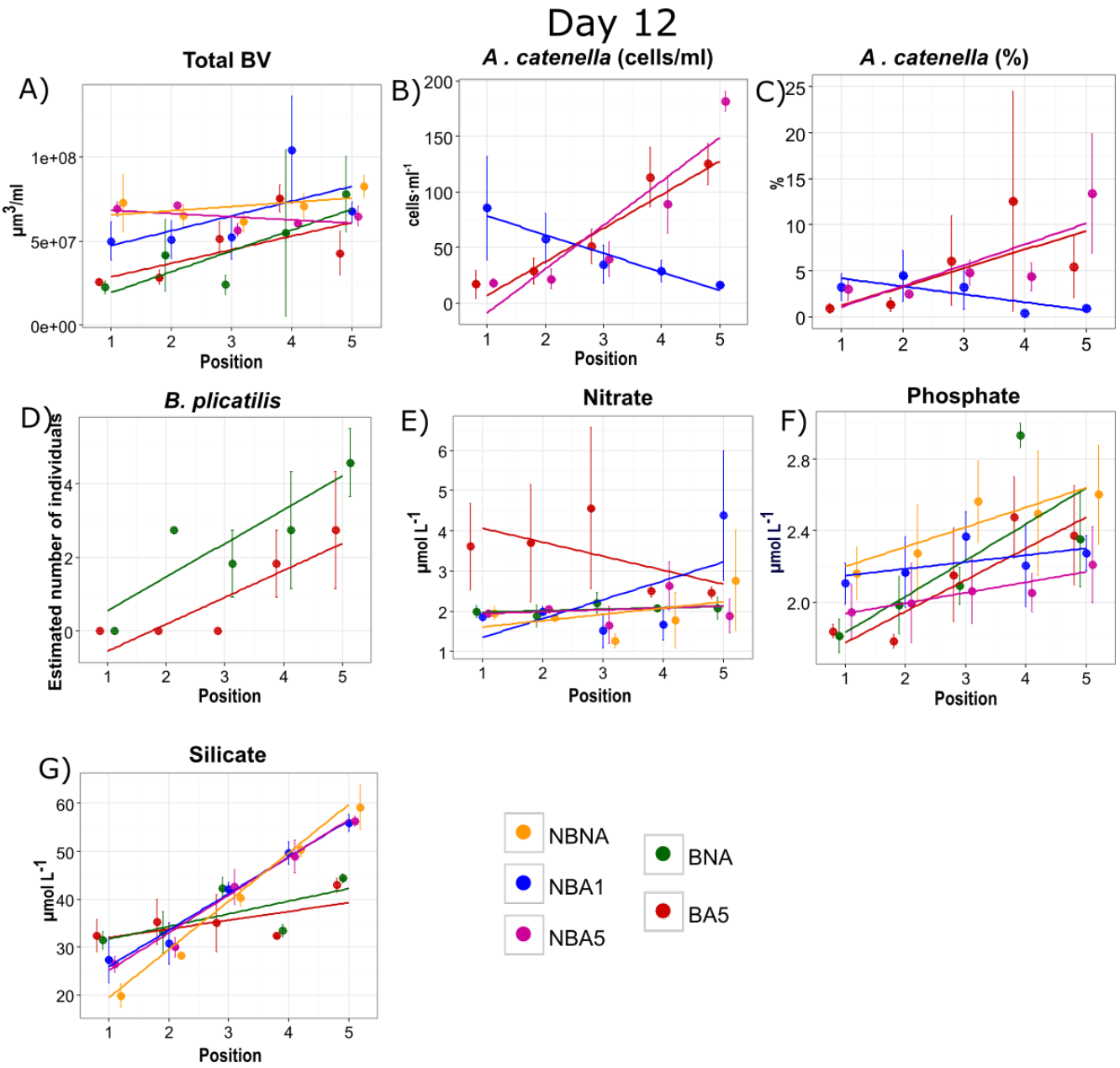

Figure 5 Day 12 mean values$^{+}_{-}$SE for A)total BV ($\mu m^3/ml$), B)*A. catenella* ($cells/ml$), C)*A. catenella* (%) D)*B. plicatilis* (estimated number of individuals) and E)Nitrate ($\mu molL^{-1}$), F)Phosphate ($\mu molL^{-1}$), G)Silicate ($\mu molL^{-1}$).

tively affected the relative abundance of *A. catenella* (table 5) in both days. The post-hoc analysis revealed that NBA1 was significantly different from NBA5 and BA5 on both days, meanwhile NBA5 and BA5 showed similar trends and values between them (table 6, 7, Fig. 5C, 6C). NBA5 and BA5 showed a higher *A. catenella* relative abundance in the input and neighbouring positions than NBA1, contradicting the predictions of *H5*.

A. catenella affected negatively to *B. plicatilis* abundance (supporting *H7*). On BA5, *B. plicatilis* was undetectable in the low nutrient concentration positions on day 12 meanwhile BNA presented *B. plicatilis* in all positions except in the lowest nutrient

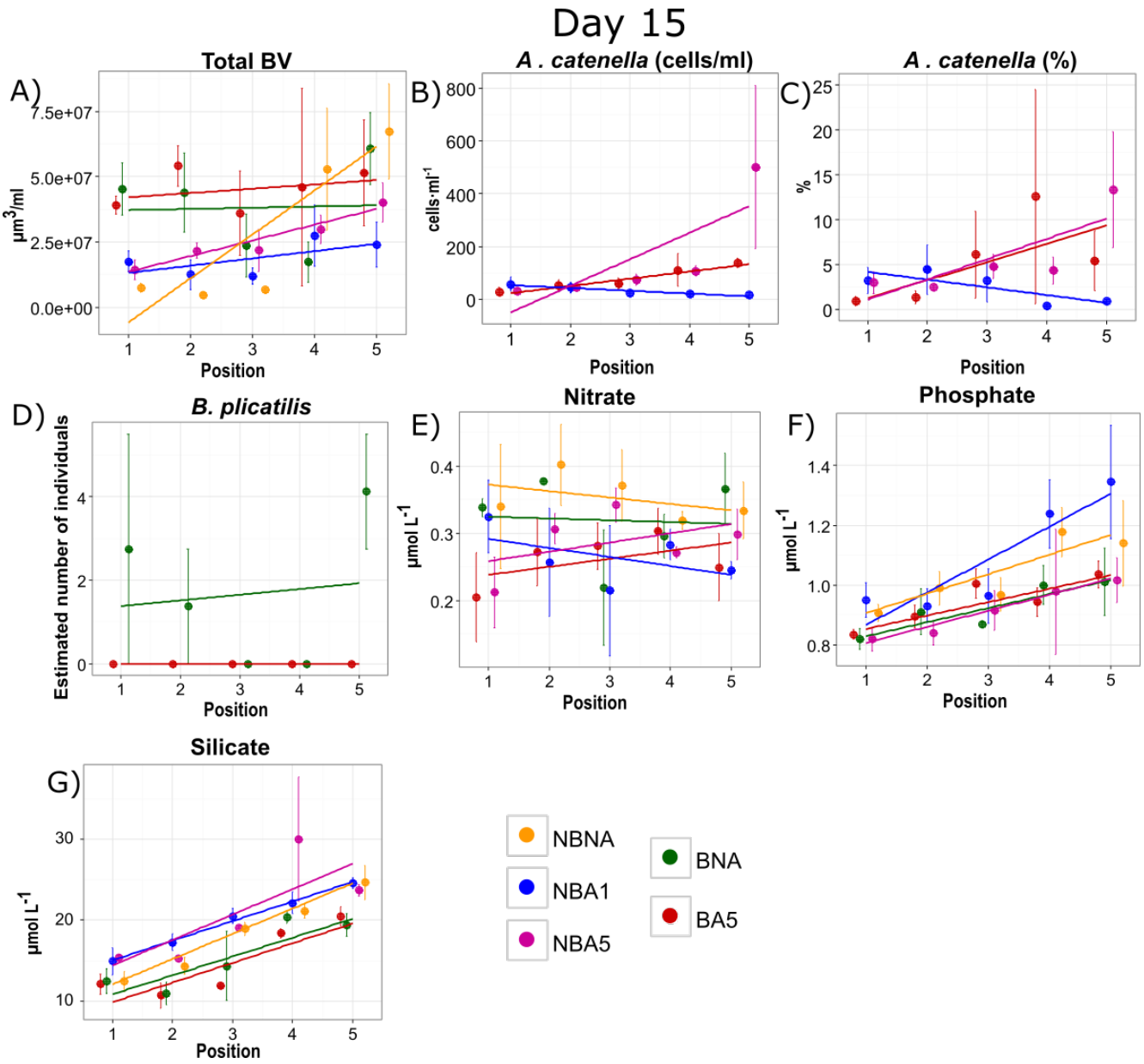

Figure 6 Day 15 mean values$^{+}_{-}$SE for A)total BV ($\mu m^3/ml$), B)*A. catenella* ($cells/ml$), C)*A. catenella* (%) D)*B. plicatilis* (estimated number of individuals) and E)Nitrate ($\mu molL^{-1}$), F)Phosphate ($\mu molL^{-1}$), G)Silicate ($\mu molL^{-1}$).

concentration position (Fig. 5D). On day 15 *B. plicatilis* was undetectable in all positions in BA5 meanwhile in BNA it was present in the highest nutrient concentration position and the two lowest nutrient concentration positions (Fig. 6D).

A. catenella and *B. plicatilis* modified the structure of the community and the distribution of the total algal BV along the gradient (supporting *H8* and *H9*). On day 12 all treatments presented a decreasing trend in the *P. micans* relative abundance distribution from high nutrients to low nutrient concentration, except for NBA5, where the relative abundance of this species increased with higher nutrient concentrations (table 5 and 6; Fig. 7A). Also, *R. abbreviata* showed increasing contributions with higher nutrient

concentrations except for BNA that showed the lowest contributions in the low nutrient concentration positions (table 5 and 6; Fig. 7A). Although on this day there was no interactive effect between treatment and position on the total alga BV (table 5), all treatments present an increasing total algal BV with increasing nutrient positions except for NBA5 that presents a decreasing non-significant trend with increasing nutrient concentration (Fig. 5A).

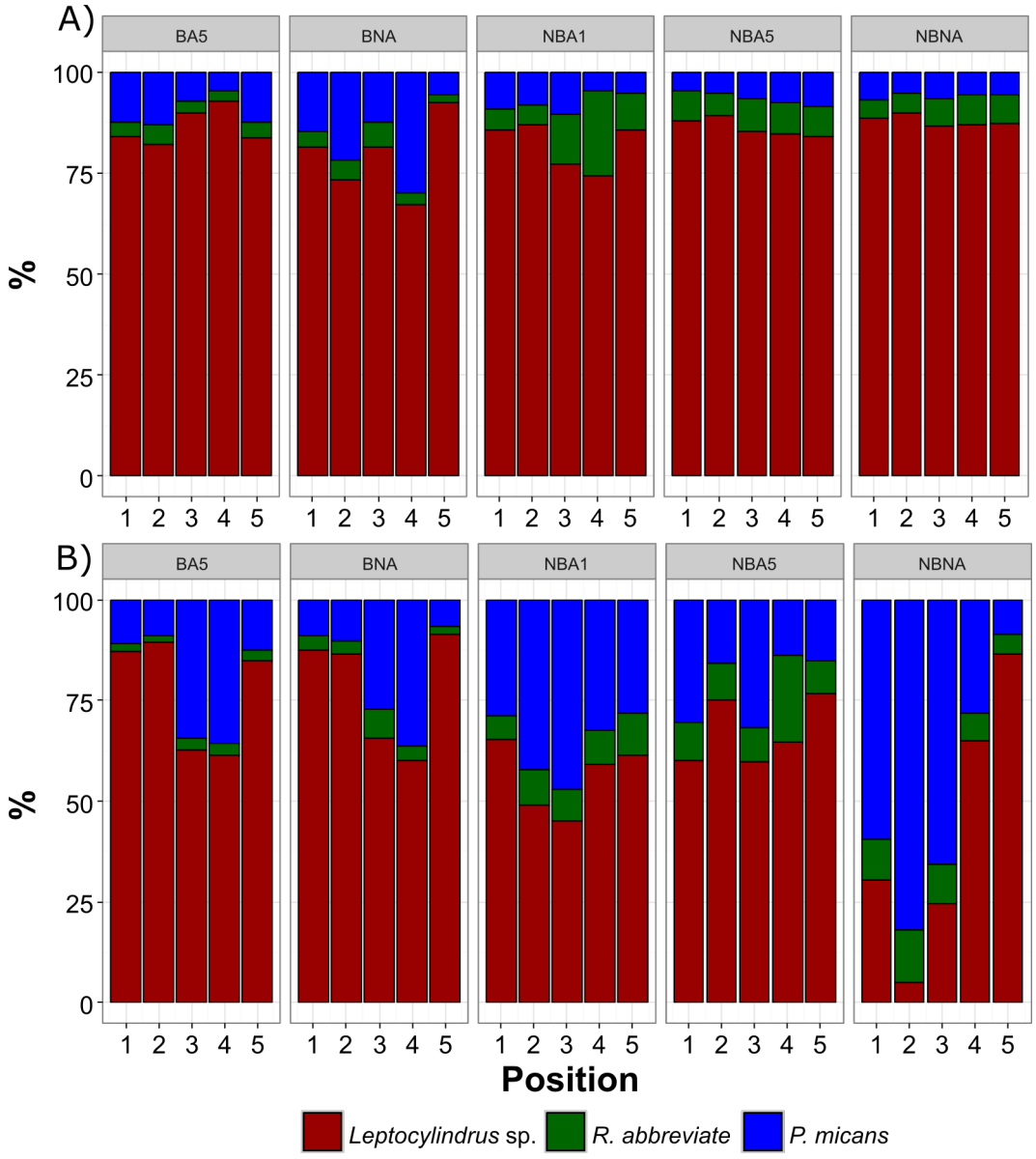

Figure 7 mean relative abundances of the phytoplankton species of the non-toxic community$^{+}_{-}$SE in A) day 12 and B) day 15.

On day 15 NBNA showed a significantly different total BV distribution along the nutrient gradient with all treatments (fig 6A, table 5 and 7). In the high nutrient positions NBNA showed similar total BV values to BNA and BA5 (treatments with *B. plicatilis*), meanwhile the total BV values on those positions were lower in NBA1 and

Table 5 p-values of the mixed model for position. Testing: total BV *A. catenella* relative abundance and the non-toxic phytoplankton species relative abundances (*Leptocylindrus* sp., *P. micans* and *R. abbreviate*).

		Day 12		**Day 15**	
Treatment	*df*	*Chisq*	*p-value*	*Chisq*	*p-value*
A. catenella (%)	2	0.96	0.617	2.12	0.346
Total BV	4	13.99	0.007**	6.31	0.17
Leptocylindrus sp. (%)	4	8.09	0.088·	6.96	0.137
P. micans (%)	4	19.36	<0.001***	5.48	0.24
R. abbreviate (%)	4	53.05	<0.001***	70.14	<0.001***
Position	*df*	*Chisq*	*p-value*	*Chisq*	*p-value*
A. catenella (%)	1	21.98	<0.001***	4.21	0.040*
Total BV	1	9.71	0.001**	12.95	<0.001***
Leptocylindrus sp. (%)	1	0.14	0.701	0.79	0.37
P. micans (%)	1	3.80	0.051·	4.59	0.032*
R. abbreviate (%)	1	1.75	0.185	0.14	0.707
Position:Treatment	*df*	*Chisq*	*p-value*	*Chisq*	*p-value*
A. catenella (%)	2	110.02	<0.001***	14.33	<0.001***
Total BV	4	6.43	0.168	13.38	<0.001***
Leptocylindrus sp. (%)	4	1.89	0.755	10.55	0.032*
P. micans (%)	4	10.30	0.035*	11.24	0.023*
R. abbreviate (%)	4	17.17	0.001**	7.87	0.096·

NBA5. In the low nutrient positions BNA and BA5 showed higher total BV values than NBNA, meanwhile NBA1 and NBA5 showed similar values to NBNA.

On day 15 there are also significant modifications in the community structure (table 5; Fig. 7B): *Leptocylindrus* sp. showed an increasing contribution with increasing nutrient concentration in NBNA, dominating only in the high nutrient positions; however, when *A. catenella* was present, this trend was weakened, and both NBA1 and NBA5 showed higher *Leptocylindrus* sp. contributions than NBNA in the low nutrient positions (being the dominant species in these positions) (table 7). *P. micans* and *R. abbreviata* contributions decreased with increasing nutrient concentrations in NBNA; in the low nutrient positions *P. micans* was the dominant species. This contrasted with the trends observed when *A. catenella* was present in NBA1 and NBA5 where the contributions of *P. micans* and *R. abbreviata* were lower than NBNA in the low nutrient positions.

B. plicatilis also affected the community structure on day 15: both BNA and BA5 present similar trends in the *Leptocylindrus* sp. and *P. micans* relative contribution along the experimental unit to NBA1 and NBA5; showing significant differences with NBNA (table 5 and 7; Fig. 7A).

Table 6 Day 12: 95% percentile bootstrap confidence interval testing of the total algal BV and the relative abundances of *A. catenella*, *Leptocylindrus*,*P. micans*. Significant values are market in bold numbers.

Treatments	*A. catenella*	*P. micans*	*R. abbreviata*
BA5-BNA	-	-	**0.1093, 0.4820**
BA5-NBA1	**-1.296, -0.816**	-	-
BA5-NBA5	-	**0.0368, 0.5736**	-
BA5-NBNA	-	-	-
BNA-NBA1	-	-	**0.1768, 0.5725**
BNA-NBA5	-	**0.1245, 0.6905**	-0.0042, 0.4179
BNA-NBNA	-	-	**0.0645, 0.4712**
NBA1-NBA5	**1.017, 1.542**	-	
NBA5-NBNA	-	-0.1258, 0.3966	-

Table 7 Day 15: 95% percentile bootstrap confidence interval testing of the total algal BV and the relative abundances of *A. catenella*, *Leptocylindrus*,*P. micans*. Significant values are market in bold numbers.

Treatments	*A. catenella*	Total BV	*Leptocylindrus*	*P. micans*
BA5-NBA1	**-0.1093, -0.0261**	-	-	-
BA5-NBNA	-	**5496424, 23677156**	**0.0580, 0.2806**	**-0.9303, -0.1652**
BNA-NBNA	-	**5108151, 24471189**	**0.0385, 0.2839**	**-1.0338, -0.1951**
NBA1-NBA5	0.0291, 0.1115	-	-	-
NBA1-NBNA	-	**4030774, 21421682**	**0.0244, 0.2602**	**-0.7702, -0.0275**
NBA5-NBNA	-	**2490237, 19761235**	**0.0040, 0.2341**	**-0.7704, -0.0227**

3.3 Model analysis

A first round of numerical simulations without dispersal was performed to analyse how allelopathy affects to the final equilibrium in high and low nutrient concentrations. In the simulation without allelopathy, the non-toxic algae dominated in high and low nutrient concentrations (Fig. 8B and D).

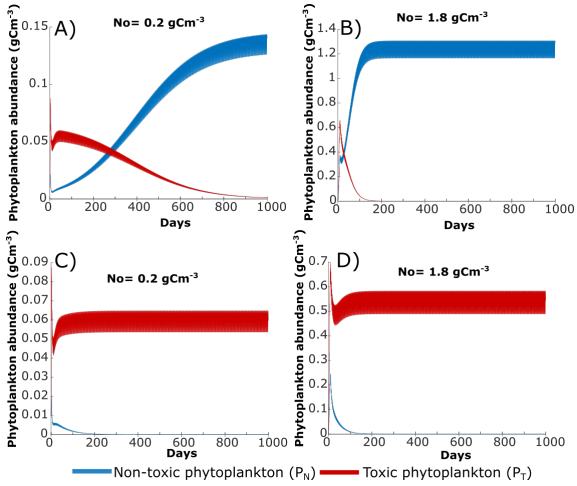

Figure 8 Concentrations of P_N (blue) and P_T (red) without dispersal. Without allelopathy ($\theta_{P_N} = 0$): A) P_N and P_T (N_o=0.2gCm^{-3}) B) P_N and P_T (N_o=1 gCm^{-3}). With allelopathy: C) P_N and P_T (N_o=0.2gCm^{-3}) D) P_N and P_T (N_o=1 gCm^{-3}).

When allelopathy is included to the system, the toxic phytoplankton dominated at both nutrient concentrations (Fig. 8F and G). The toxic phytoplankton was favoured at the beginning for the lower grazing pressure and increased the concentration faster than the non-toxic phytoplankton. Since the allelopathic effect is density dependent, this bloom inhibited the non-toxic phytoplankton growth.

A second round of numerical simulations were performed including allelopathy and dispersal in the system. The concentration of each phytoplankton species at the equilibrium was analysed increasing the dispersal time as described in the methods. As in the experiment, two different starting positions were considered for the toxic phytoplankton: at low nutrient concentration and at high nutrient concentration.

Both starting positions showed same dynamics: When dispersal time was low, the toxic phytoplankton dominated in all positions (T_2<3.13 hours day^{-1}, P_T starting position N_o=0.2gCm^{-3} and T_2<4.99 hours day^{-1}, P_T starting position N_o=1gCm^{-3}). As dispersal time increased, there was a shift in dominance from toxic phytoplankton to non-toxic phytoplankton. These results confirm the *H10*.

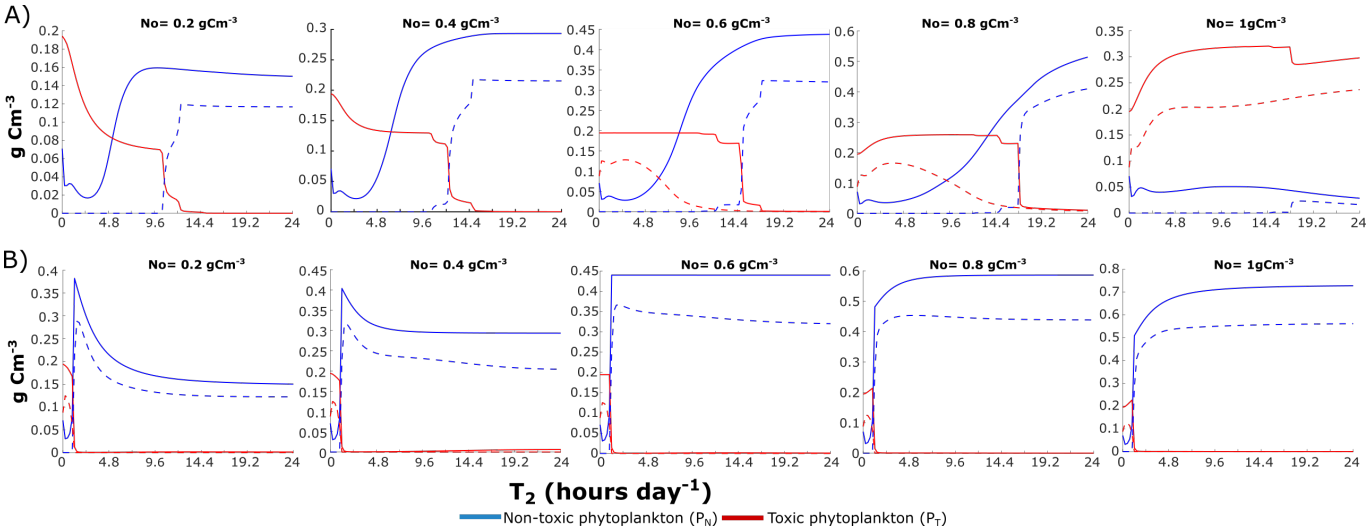

Figure 9 Variations in the equilibrium values of P_N (blue) and P_T (red) as the hours of dispersal increases (T_2) where the other parameter values are the same as in table 2. Each graph in A) and B) represents a different community in the nutrient gradient, from low nutrient concentration (left) to high nutrient concentration (right). The continuous and dashed line represents the maximum and minimum values in the equilibrium respectively. A) starting position for P_T at high nutrient concentration (N_o=1gCm^{-3}). B) starting position for P_T at low nutrient concentration (N_o=0.2gCm^{-3}).

4 DISCUSSION

This research investigated the population dynamics of *A. catenella* and its interaction with a plankton metacommunity. The results were analysed both regionally and locally, and showed that *A. catenella* allelopatic effects on the non-toxic community were only significant at a local scale, after nutrient depletion and when the population of the non-toxic community was decreasing. Table 8 summarizes the hypotheses made at the beginning of this experiment and its confirmation or rejection.

4.1 Regional dynamics

The starting concentration of *A. catenella* at a regional scale was ∼30cells ml^{-1}; since the typical bloom in this species is 17cells ml^{-1} (Jester et al. [2009b]), the set up concentration corresponded to a potential bloom concentration. The *A. catenella* increase in cell concentration showed that *A. catenella* can increase its concentration in a heterogeneous landscape with different nutrient conditions.

The initial inoculation position did not have an effect on *A. catenella* relative contribution to the community (contradicting *H1*). *A. catenella* is a better competitor

Table 8 Summary of the hypotheses tested on this experiment.

Hypotheses	Statements	Result
Regional scale		
H1	∘*A. catenella* relative abundance will be higher when inoculated at low nutrient concentration.	Rejected
H2	∘*A. catenella* decreases the total BV.	Rejected
	∘*A. catenella* alters the community composition.	Rejected
H3	∘ *A. catenella* reduces *B. plicatilis* abundance.	Rejected
H4	∘*B. plicatilis* reduces the total algal BV and *A. catenella* relative abundance.	Rejected
	∘*B. plicatilis* alters the phytoplankton community structure.	Confirmed
Local scale		
H5	∘The total BV of the non toxic community increases with increasing nutrient concentration.	Confirmed
H6	∘*A. catenella* disperses through the metacommunity.	Confirmed
	∘*A. catenella* has a higher BV and contribution to the community when it is inoculated at low nutrient concentrations.	Rejected
H7	∘ *A. catenella* decreases *B. plicatilis* abundance.	Confirmed
H8	∘*A. catenella* decreases the total algal BV.	Confirmed
	∘*A. catenella* alters the community structure.	Confirmed
H9	∘*B. plicatilis* decreases the total algal BV.	Confirmed
	∘*B. plicatilis* decreases *A. catenella* relative abundance.	Confirmed
	∘*B. plicatilis* alters the community structure.	Confirmed
Model		
H10	∘The toxic species will dominate when there is low dispersal time.	Confirmed

when nutrients are not plentiful (Kudela et al. [2008]); however, in the experiment the concentration of the inoculation position did not have a significant effect on the *A. catenella* relative contribution (Fig. 3C). This could be explained because the rapid increase of the non-toxic community outcompeted *A. catenella* the first days of the experiment.

The presence of *A. catenella* did not have a significant effect on either the total algal BV nor the community structure (Fig. 3D and 4). This result indicates that no allelopathic effect could be observed at a regional scale despite the high concentration of *A. catenella* (contradicts *H2*). This result match with previous observations demonstrating that the intensity of the allelopathic effects not only depends on the concentration of the donor species but also on the density of the target species (Fistarol et al. [2004], Tillmann et al. [2007]). In this case, the dominating species *Leptocylindrus* has very fast growth rates (Ajani et al. [2016]) that probably compensated any potential harmful effect on this species.

There was not a clear harmful effect of *A. catenella* on *B. plicatilis* (Fig. 3E) (rejects *H4*). *B. plicatilis* has been proposed as a suitable model organism for detecting potential harmful effects by toxic algae (Yan et al. [2009]). In the present study, the treatment with *A. catenella* (BA5) showed less *B. plicatilis* abundance than the treatment without *A. catenella* (BNA); especially in day 15, when *B. plicatilis* was undetected in BA5 but present in BNA. However, from day 15 to the end of the experiment *B. plicatilis* showed a constant increase in both treatments, without any clear abundance differences between them.

B. plicatilis had no grazing effect on *A. catenella* since no significant reduction of *A. catenella* was observed when *B. plicatilis* was present (Fig. 3C), rejecting *H4*. This result does not match the general belief that grazing pressure is an important regulator of HAB species concentration (Yoo et al. [2013], Jeong et al. [2010], Petitpas et al. [2015]). A possible explanation for this result is that in general, the contributions of *A. catenella* were really low (5-15%); reducing the chances for *A. catenella* to get grazed. *B. plicatilis* could only affect to *A. catenella* if it showed a preference for this species, as it did for *R. abbreviata*, whose contribution was significantly reduced in the presence of *B. plicatilis* (supporting *H4*).

4.2 Local dynamics

The total total BV increased with increasing nutrient concentration position with the sole exception of NBA5 on day 12 despite the lack of a nitrate gradient (supporting *H5*; Fig. 5A and 6A). Nitrate is often the limiting nutrient in marine systems; however, it does not drive the distribution of the total BV through the gradient, probably due to the storage of nutrients in the inside of the cell and the gradient distribution of the rest of the nutrients (Fig. 5E, F, G and 6E, F, G) (Dagenais-Bellefeuille and Morse [2013], Maguer et al. [2007], Smalley et al. [2003], Cembella et al. [1982]).

The *A. catenella* population dispersed effectively to all flasks within the meta-communities, always in close values to typical bloom concentrations (17cells ml^{-1}; Jester et al. [2009b])(supporting *H6*). The *A. catenella* maximum concentration was always in the input position and always remained in close values to the initial concentrations (Fig. 5B and 6B). On day 15, after the nutrient drop and the offset of the diatom bloom, *A. catenella* contributions increased from a 5% to a 15% in the inoculation positions of BA5 and NBA5, meanwhile in NBA1 contribution remained around the 5% (Fig. 6B, E, F, G). These results match with the general knowledge that *A. catenella* is a better competitor at low nutrient concentrations (relative abundance only increased after the decrease in nutrients and competitors), but also showed that this increased only happened in the high nutrient concentration inoculation position (NBA5 and BA5). This could be explained because dinoflagellates can accumulate nutrients and use them when there is nutrient scarce in the environment (Dagenais-Bellefeuille and Morse [2013], Maguer et al. [2007], Smalley et al. [2003], Cembella et al. [1982]). As it was also observed at a regional scale, this indicates that previous nutrient conditions could determine future blooming events; in other words, *A. catenella* can be more competitive and higher chances of blooming if the low nutrient concentration environment is preceded by high nutrient concentration.

A. catenella had a harmful effect on *B. plicatilis* that modified its distribution along the gradient, making microzooplankton undetectable in positions 1-3 on day 12 and totally undetectable in all positions on day 15 (Fig. 5D and 6D) (supporting *H7*). Busch [2016] found a correlation between increasing *A. catenella* concentrations and *B. plicatilis* mortality. The results of day 12 however, indicate that *B. plicatilis* mortality was higher under low *A. catenella* relative abundances. A possible explanation for this result is that under low nutrient concentration there was also a lower algal BV than under high nutrient

concentration, making *B. plicatilis* under food limitation more susceptible to *A. catenella* allelopathy.

A. catenella and *B. plicatilis* modified significantly the total BV and community structure (supporting *H8* and *H9*). This effect was not significant on day 12 (no significant interaction between treatments and nutrient effect); however, there was a non-significant trend in NBA5 that indicates the total algal BV increases with decreasing *A. catenella* relative contribution and not with increasing nutrient concentration, indicating that not only the nutrient conditions, but also allelochemicals determined the patterns observed (fig. 5A and B). This non-significant trend matches with the general knowledge that allelopathic effect depends on the *A. catenella* relative abundance (Tillmann et al. [2008]).

On day 15, the treatments with *A. catenella* (NBA1 and NBA5) had significant interactions with the control NBNA (Fig. 6A) on the total BV. In the low nutrient concentration positions NBA1 and NBA5 showed similar BV to NBNA, indicating that the low nutrient concentration limited the algal growth, masking any potential allelopathic effect. In the high nutrient concentration positions both NBA1 and NBA5 showed lower BV than NBNA due to the allelopathic effect of *A. catenella*. The higher *A. catenella* relative abundance in NBA5 high nutrient concentration positions compared to NBA1 did not result on different trends on the total BV distribution (Fig. 6A and B). Thus, in the high nutrient concentration positions certain growth was allowed but it was limited by the allelopathic effect. It is important to note that in the high nutrient positions, NBA5 had a higher concentration and relative contribution of *A. catenella* than NBA1, but still there were no significant differences in the allelopathic effect between treatments (total BV). These results shows how the allelopathic effect is not only determined by the concentration of the donor species (Tillmann et al. [2008]), but also by the environmental conditions.

The presence of *A. catenella* also altered the community structure: in NBNA, the low nutrient concentration positions presented a shift in dominance from diatoms (*Leptocylidrus* sp.) to dinoflagellates (*P. micans*) (Fig. 7A). However, *A. catenella* favoured the diatom dominance even in the low nutrient concentration positions because *P. micans* is strongly inhibited by allelochemicals (Ji et al. [2011]) meanwhile *Leptocylindrus* sp. is not very susceptible to it (Fistarol et al. [2004]).

The *B. plicatilis* also affected the community structure and total BV on day 15 (Fig. 6A and Fig. 7B). *B. plicailis* can select the prey (Chotiyaputta and Hirayama [1978]) and in the low nutrient concentration positions *B. plicatilis* reduced the relative contribution of *P. micans*, favouring *Leptocylindrus* sp. dominance. Thus, the depletion of *P. micans* reduced the nutrient competition, favouring *Leptocylindrus* sp. to growth increasing the total BV in the low nutrient positions compared to NBNA. On the other hand, in the high nutrient positions, both BNA and BA5 showed similar total BV to NBNA (and thus higher than NBA1 and NBA5). Since BA5 and BNA showed a similar trend on the total BV, it can be interpreted that *A. catenella* did not have any significant effect on the non-toxic community in BA5. This could also be explained again by the preference of *B. plicatilis* for *P. micans*: the grazing pressure on *P. micans* reduced the nutrient competition allowing *Leptocylindrus* sp. to grow overcoming the allelopathic effect. This result indicates that *B. plicatilis* can control the bloom and allelopathic effects not only by direct predation on the toxic species (Turner [2010]), but also modifying the community structure in a way that nutrient competition is reduced and the fast growing species can grow despite the allelopathy.

4.3 Model analysis

Lower dispersal time allowed the phytoplankton to increase the biomass increasing the allelopathic effect on the non-toxic phytoplankton and dominating on one community before dispersing to the neighbouring communit (Fig. 9) (supporting *H10*). Mukhopadhyay and Bhattacharyya [2006] proved theoretically that at low constant dispersal, zooplankton can control algal blooms. These results however show that when allelopathy is included, interrupted dispersal could favour the bloom formation in a system that would remain stable under continuous dispersal. Roy [2009] proved theoretically that an isolated community (no dispersal) in a homogeneus medium can present coexistence between two species competing for a single nutrient if one of the two species has a sufficiently strong allelopathic effect on the other. In this study, when the toxic phytoplankton dominated due to the allelopathy, the two phytoplankton species coexisted in the equilibrium. This complements Roy [2009] results, demonstrating theoretically that coexistence in a heterogeneus metacommunity with dispersal was also possible.

The ocean hydrology is based on more complex dynamics than dispersal. Water

movements involve currents, eddies, upwellings, etc. Yet, some field observations have reported that temporary retention of water movements can create an incubation region for bloom formation that would later be extended to larger areas (Ryan et al. [2009]).

5 CONCLUSION

In conclusion, this study shows that at a regional scale *A. catenella* can increase the abundance through a heterogeneous landscape by dispersing along a metacommunity. At a local scale the allelopathic effect of *A. catenella* not only depends on its relative abundance, but also on the environmental conditions (in this case nutrient concentration). Also, microzooplankton can offset the allelopathic effect on a phytoplankton metacommunity by modifying the community structure. The modelling approach indicated that interrupted dispersal could favour harmful algal blooms occurrence due to the accumulation of biomass.

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7 APPENDIX 1

f/2 Medium (Guillard and Ryther [1962])

Volume	Compound	Concentration
1ml	NaNO3	882,5 $\mu molL^{-1}$
1ml	NaH2PO4 * H_2O	36 $\mu molL^{-1}$
1ml	Na2SiO3 * 9H_2O	105,56$\mu molL^{-1}$
1ml	f/2 Trace Metal Solution	See recepy below
1ml	f/2 Vitamin Solution	See recepy below

f/2 Trace metal solution

Volume/Weight	Compound	Concentration
3,15 g	FeCl3 * 6H_2O	-
4,36 g	Na2EDTA * 2H_2O	-
1 ml	CuSO4 * 5H_2O	9,8 gL^{-1} dH_2O
1 ml	Na2MoO4 * 2H_2O	6,3 gL^{-1} dH_2O
1 ml	ZnSO4 * 7H_2O	22 gL^{-1} dH_2O
1 ml	CoCl2 * 6H_2O	10 gL^{-1} dH_2O
1 ml	MnCl2 * 4H_2O	180 gL^{-1} dH_2O

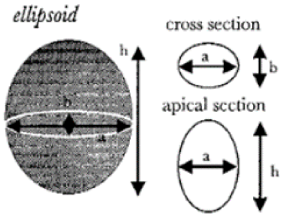
f/2 Vitamin solution

Volume/Weight	Compound	2 **Stock Solution**
1 ml	Vitamin B12 (cyanocobalamin)	1 gL^{-1} dH2O
10 ml	Biotin	0,1gL^{-1} dH2O
200 mg	Thiamine * HCl	-

8 APPENDIX 2

The biovolume of each species was calculated by the simplification of each species to a simple geometrical form as described in Hillebrand et al. [1999]. The biovolume used in the calculations was the result of the average of 30 samples. Find below the geometrical form and formulas used for each species.

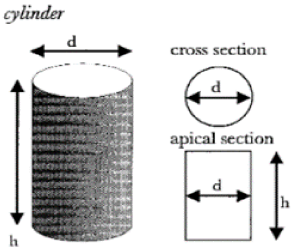
Alexandrium catenella:



This body is subspherical with three different dimensions (prolate spheroid with elliptical cross-sections).

$$V = \frac{\pi}{6} \cdot a \cdot b \cdot h$$

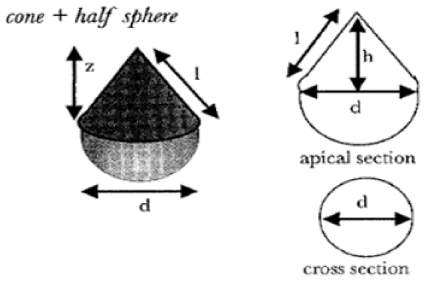
Leptocylindrus sp.:



$$V = \pi \cdot r^2 \cdot h = \frac{\pi}{4} \cdot d^2 \cdot h$$

$$A = 2 \cdot \pi \cdot r^2 + 2 \cdot \pi \cdot r \cdot h = \pi \cdot d \cdot (\tfrac{d}{2} + h)$$

Prorocentrum micans and *Rhodomonas abbreviata*:



$$V = \frac{1}{3} \cdot \pi \cdot r^2 \cdot z + \frac{1}{2} \cdot \frac{4}{3} \cdot \pi \cdot r^3$$
$$= \frac{\pi}{12} \cdot d^2 \cdot (z + d)$$

$$A = \pi \cdot r \cdot l + 2 \cdot \pi \cdot r^2$$
$$= \frac{1}{2}\pi \cdot d \cdot l + \frac{1}{2}\pi \cdot d^2$$
$$= \frac{1}{2}\pi \cdot d \cdot (l + d)$$

9 APPENDIX 3

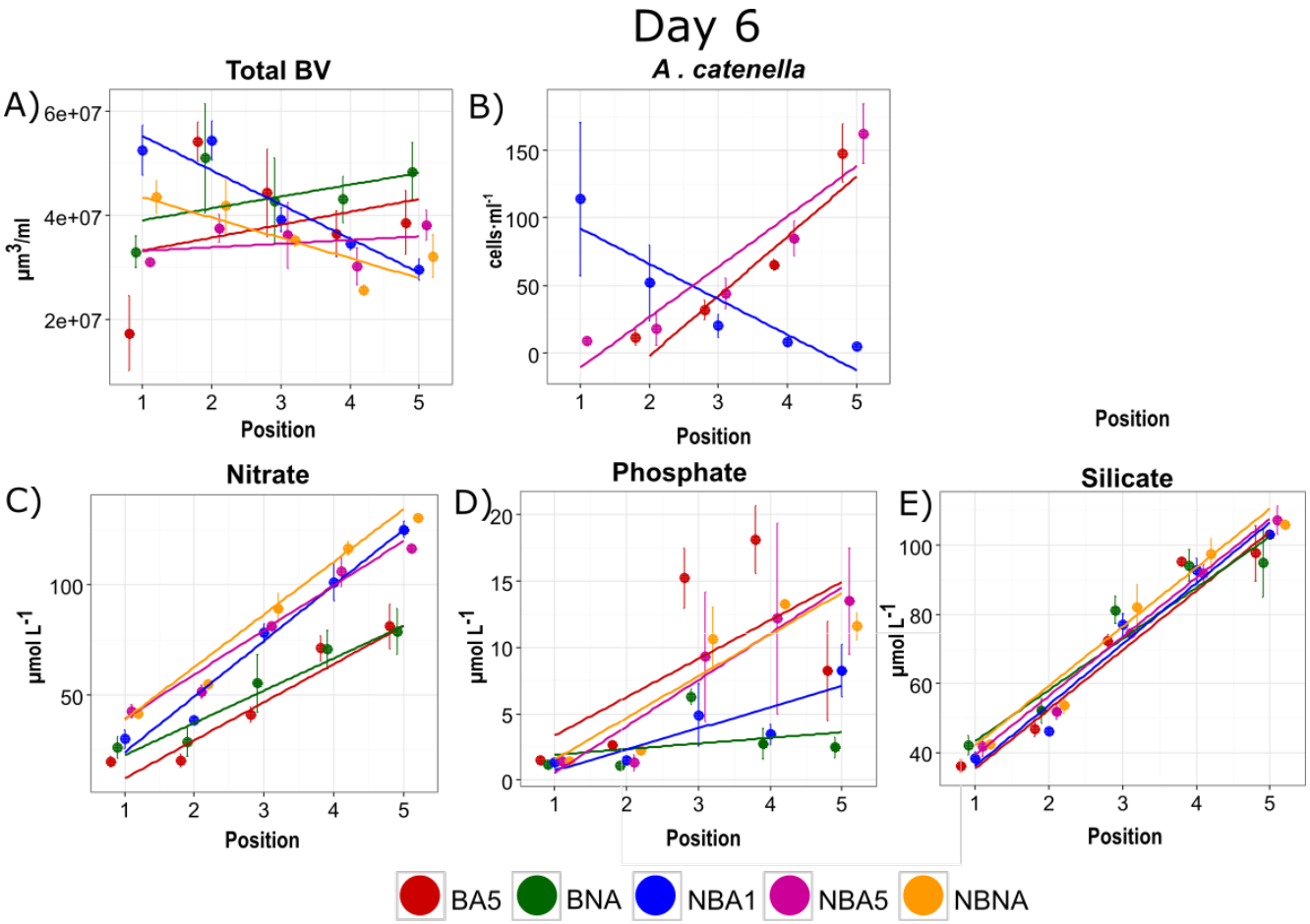


Figure 10 Day 6 mean values$^{+}_{-}$SE for A)total BV ($\mu m^3/ml$), B)*A. catenella* ($cells/ml$), C)Nitrate ($\mu molL^{-1}$), D)Phosphate ($\mu molL^{-1}$), E)Silicate ($\mu molL^{-1}$).

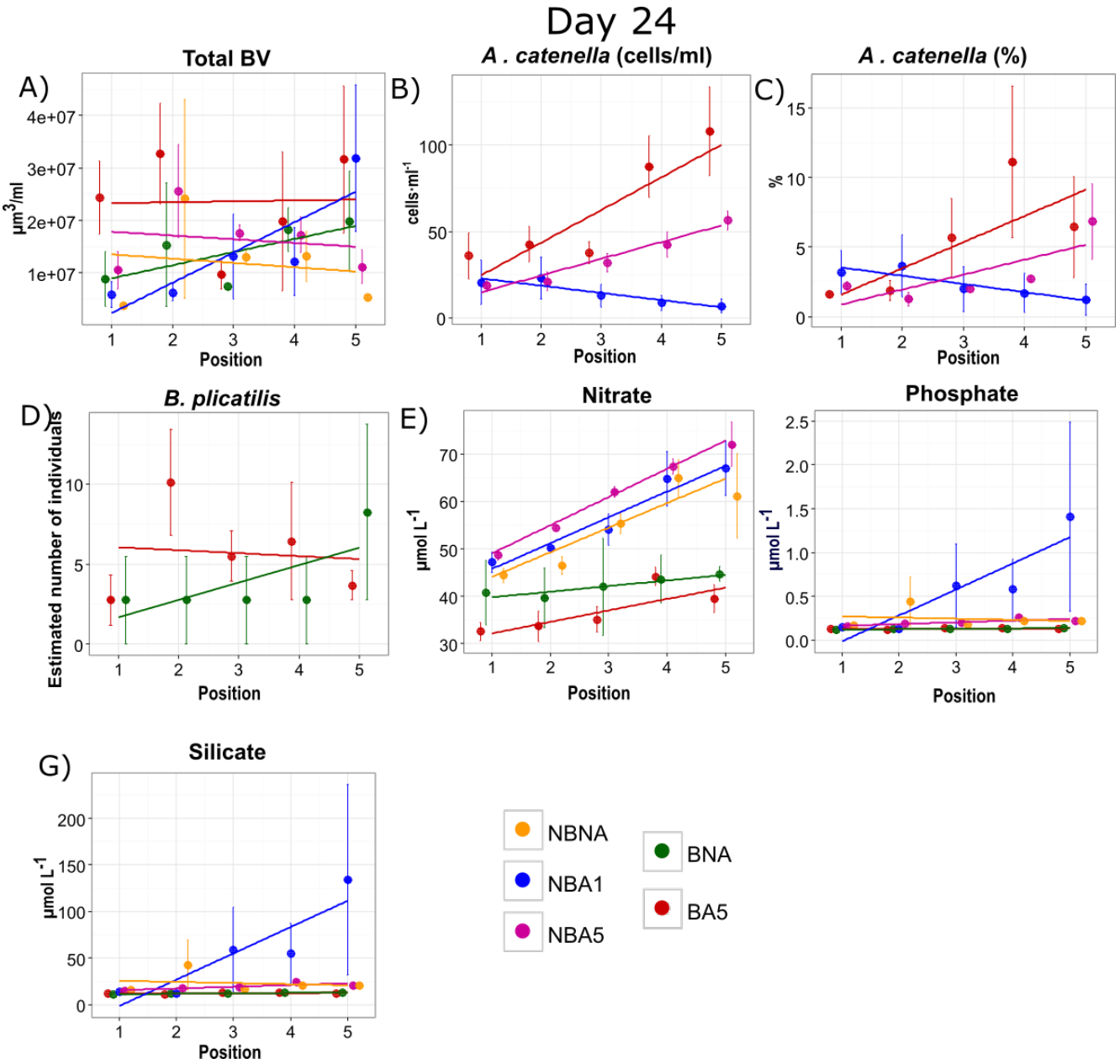


Figure 11 Day 24 mean values$^{+}_{-}$SE for A)total BV ($\mu m^3/ml$), B)*A. catenella* ($cells/ml$), C)*A. catenella* (%) D)*B. plicatilis* (estimated number of individuals) and E)Nitrate ($\mu molL^{-1}$), F)Phosphate ($\mu molL^{-1}$), G)Silicate ($\mu molL^{-1}$).

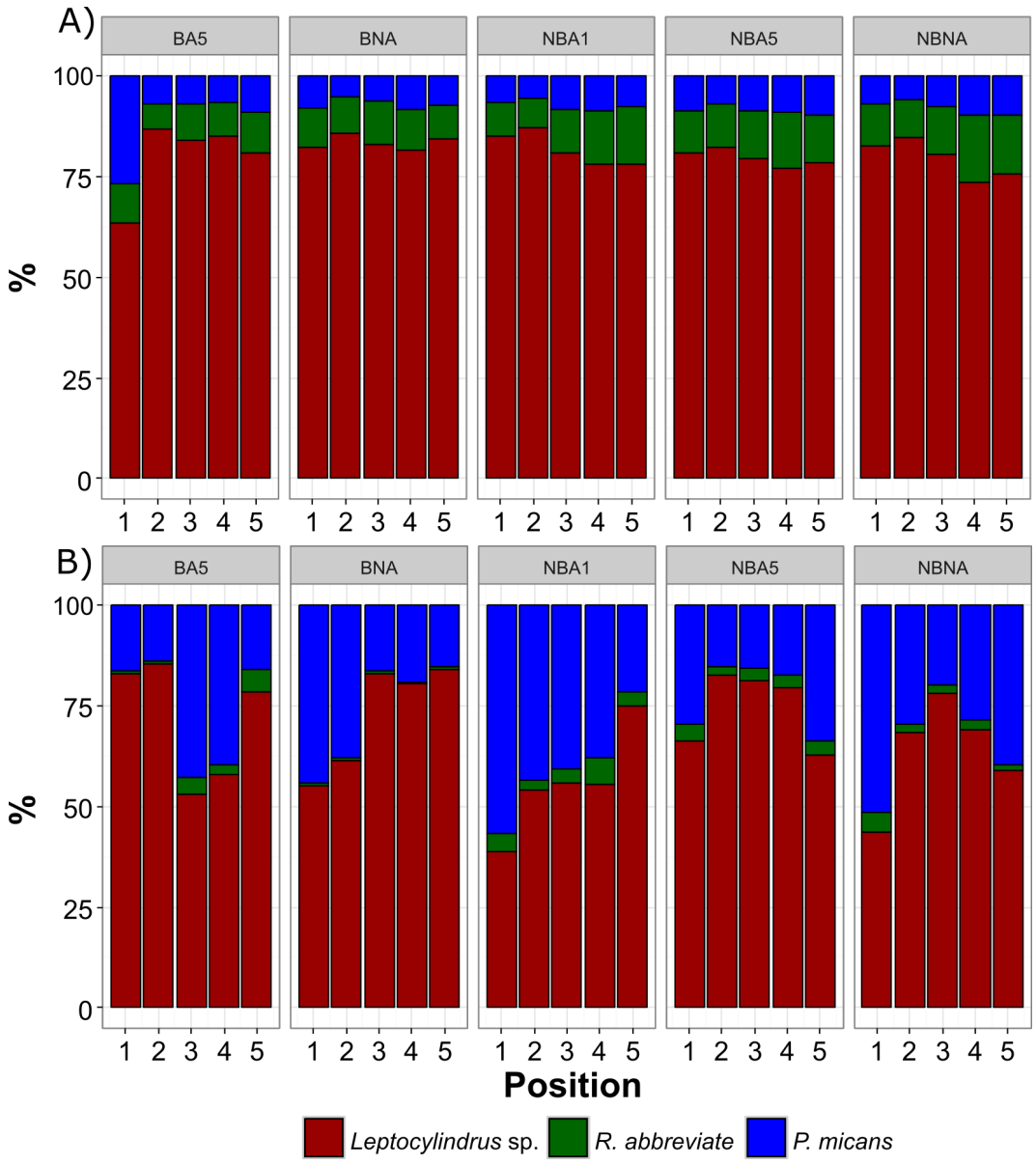


Figure 12 mean relative abundances of the phytoplankton species of the non-toxic community$^{+}_{-}$SE in A) day 6 and B) day 24.