

# High predictability of spring phytoplankton biomass in mesocosms at the species, functional group and community level

BARBARA BAUER<sup>\*,†</sup>, ULRICH SOMMER<sup>†</sup> AND URSULA GAEDKE<sup>\*</sup>

<sup>\*</sup>Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany

<sup>†</sup>Helmholtz Centre for Ocean Research Kiel (GEOMAR), Kiel, Germany

## SUMMARY

1. Models aim to predict phytoplankton dynamics based on observed initial conditions and a set of equations and parameters. However, our knowledge about initial conditions in nature is never perfect. Thus, if phytoplankton dynamics are sensitive to small variations in initial conditions, they are difficult to predict.

2. We used time-series data from indoor mesocosm experiments with natural phyto- and zooplankton communities to quantify the extent to which small initial differences in the species, functional group and community biomass in parallel treatments were amplified or buffered over time. We compared the differences in dynamics between replicates and among all mesocosms of 1 year.

3. Temperature-sensitive grazing during the exponential growth phase of phytoplankton caused divergence. In contrast, negative density dependence caused convergence.

4. Mean differences in biomass between replicates were similar for all hierarchical levels. This indicates that differences in their initial conditions were amplified to the same extent. Even though large differences in biomass occasionally occurred between replicates for a short time, dynamics returned to the same path at all hierarchical levels. This suggests that internal feedback mechanisms make the spring development of phytoplankton highly predictable.

*Keywords:* divergence, hierarchical level, mesocosms, predictability, replicates

## Introduction

Phytoplankton constitutes almost 50% of global primary production and is the base of the pelagic food web. Thus, forecasting the yearly development of phytoplankton communities in the future is of high importance. Ecologists have used a number of models to represent and predict phytoplankton community dynamics. A model prediction is defined as the evaluation of the future state of a system based on a set of initial conditions, forcing and the mathematical representation of relevant ecological processes. Based on model predictions, using the best available data, ecologists are able to give forecasts, that is, probabilistic statements of the future state of a system (Luo *et al.*, 2011). To assess the reliability of model

predictions for the purpose of forecasting, we need not only to estimate our uncertainty about initial conditions, forcing and other factors influencing dynamics but also to assess the sensitivity of the dynamics to each of these factors. Species composition is harder to monitor than abiotic forcing; thus, if the community biomass of systems with a similar initial species composition and under the same forcing shows different dynamics (i.e. diverge from each other over time), they are unpredictable, that is, the uncertainty of the predictions made about them is large.

Historical effects (e.g. microevolution, founder effect) or previous differences in environmental forcing cause natural variability in total biomass and species composition among similar phytoplankton communities. Divergence or convergence of the total biomass among these

Correspondence: Barbara Bauer, Helmholtz Centre for Ocean Research Kiel (GEOMAR), Düsternbrooker Weg 20, D-24105 Kiel, Germany.

E-mail: bauerb@uni-potsdam.de

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1 communities depends on the relevance of negative den-  
 2 sity-dependent feedback processes acting upon it. For  
 3 example, competition for light or nutrients and density-  
 4 dependent predation (Morin, 1995) regulate the biomass  
 5 of the whole phytoplankton community, regardless of its  
 6 species composition. Thus, if negative density-dependent  
 7 processes play an important role in community regula-  
 8 tion, the biomass development is influenced more by light  
 9 availability or the presence of a generalist predator than  
 10 by the exact initial phytoplankton species composition. In  
 11 this case, the total biomasses of similar communities are  
 12 expected to converge. Hence, their fate is predictable with  
 13 models incorporating a few regulatory mechanisms (Til-  
 14 man, 1990).

15 Individual species are not only affected by community-  
 16 level regulation but also by species-specific density-  
 17 dependent regulation such as selective predation and  
 18 host-specific pathogens. These processes are sensitive to  
 19 the presence and absence of interacting species, that is,  
 20 they are highly context-dependent (Holt, 1977). Thus,  
 21 species dynamics were proposed to be less predictable  
 22 than community dynamics (Dakos *et al.*, 2009). Individual  
 23 species and functional groups might differ in their  
 24 predictability based on the strength of the negative  
 25 density-dependent feedbacks regulating them. For exam-  
 26 ple, smaller algae, grazed by protozoan predators with  
 27 short generation times and high growth rates, are less  
 28 likely to reach high densities than larger algae, grazed by  
 29 mesozooplankton with complex life cycle and low growth  
 30 rates.

31 Clearly, there is no strict line between processes acting  
 32 on the species vs. the community level. For example,  
 33 different species react differently to nutrient concentra-  
 34 tions owing to their different nutrient requirements. Thus,  
 35 how much a given nutrient concentration limits the  
 36 growth rate at the community level depends on  
 37 the species composition as well as on the biomass of the  
 38 community.

39 For a better understanding of the processes driving  
 40 changes in biomass, ecologists often study the dynamics  
 41 of process rates. The production-to-biomass (P/B) ratio  
 42 characterises phytoplankton turnover. It is an often-  
 43 studied process rate, which is determined mostly by  
 44 available light levels and total community biomass. Thus,  
 45 its predictability is probably similar to that of the  
 46 community biomass.

47 Assessing predictability at different hierarchical levels  
 48 within the phytoplankton community is crucial for  
 49 directed data collection, model selection and setting  
 50 realistic expectations towards the predictive power of  
 51 science. Comparisons of the predictability of hierarchical

levels are useful to avoid trying to predict dynamics on  
 the 'wrong' level (Rahel, 1990). In the latter case, our  
 efforts might remain futile or we set overly optimistic  
 expectations about the time needed to develop predictions  
 or management plans.

To gain insight into the mechanisms behind the  
 predictability of phytoplankton spring development, we  
 compared how the biomass of paired experimental  
 phytoplankton communities differed through time. We  
 used phytoplankton biomass data from mesocosm exper-  
 iments conducted over 5 years with early spring natural  
 communities (Sommer & Lewandowska, 2011 and liter-  
 ature cited therein). The mesocosms were run in a highly  
 controlled environment with several realistically chang-  
 ing abiotic (temperature, light) and biotic (copepod  
 grazing) forcing factors and included the complex natural  
 grazer community. The mesocosms of 1 year were started  
 with similar initial densities and composition of phyto-  
 and zooplankton and were partly subject to different  
 treatments; 28 pairs of mesocosms, the experimental  
 replicates, were run under the same environmental  
 forcing.

We tested the degree of difference in biomass among  
 the replicates and treatments depending on the hierarchi-  
 cal level (species, functional groups, entire community)  
 and its change over time (i.e. the level of divergence)  
 during planktonic succession. Additionally, we conducted  
 the same analyses on the time series of the P/B ratio of the  
 community. We hypothesised that (i) the dynamics of  
 total phytoplankton biomass differed more among all  
 mesocosms within 1 year than between replicates as  
 environmental forcing strongly influences phytoplankton  
 dynamics; (ii) divergence and difference at the commu-  
 nity level is lower than at the functional group and species  
 level; (iii) at high levels, total phytoplankton biomasses of  
 replicates converge because of strong density dependence;  
 and (iv) divergence and difference of the P/B ratio is  
 similar to that of community biomass.

## Methods

### *The Kiel mesocosms*

The data used in this analysis were obtained from  
 mesocosm (1400 L, 1 m depth) experiments conducted  
 over 5 years with early spring phyto- and zooplankton  
 communities from the Kiel Fjord, Western Baltic Sea,  
 Germany. The mesocosms were filled simultaneously  
 with unfiltered water from the fjord, which contained  
 overwintering populations of phytoplankton, bacteria,  
 protozoans and mesozooplankton larvae. Larger

1 mesozooplankton (mainly copepods) obtained from net  
 2 catches from the fjord were added at natural abundance  
 3 (2005–2008 experiments) or in three different abundances  
 4 (2009 experiment). From February to May 2005, 2006 (two  
 5 experiments) and 2007 eight indoor mesocosms were run  
 6 under four different temperature regimes (four pairs of  
 7 replicates for each year). In 2008 and 2009, twelve  
 8 mesocosms (six pairs of replicates) were run under two  
 9 temperature regimes and three light regimes (2008) or  
 10 started with three different copepod densities (2009)  
 11 (Table 1). The mesocosms were gently mixed by a  
 12 propeller to assure a homogeneous distribution of the  
 13 plankton. Temperatures followed the observed seasonal  
 14 course of the Kiel Bight, the coldest ('baseline') corre-  
 15 sponding to the decadal average 1993–2002 and the three  
 16 others with +2, +4 and +6 °C temperature elevation above  
 17 the baseline from the beginning until the end of February.  
 18 After that, the temperature difference between the treat-  
 19 ments was reduced by 0.25 °C per month to mimic the  
 20 less pronounced warming later in the year. The day-  
 21 length was adjusted to natural conditions. The light  
 22 regime followed the natural solar irradiance ( $I_0$ ), which  
 23 was calculated from astronomic models for each day  
 24 (Brock, 1981) and reduced in the range of 16–100% in the  
 25 various experiments (for details about the experimental  
 26 set-up see Sommer *et al.*, 2007; Sommer & Lengfellner,  
 27 2008; Lewandowska & Sommer, 2010; Sommer & Lew-  
 28 andowska, 2011). Irradiance increased 11-fold during the  
 29 experiments.

30 Phytoplankton were sampled three times per week  
 31 from mid-depth (0.5 m) of the well-mixed mesocosms.  
 32

33 **Table 1** Overview of the experimental treatments. 1-factor experi-  
 34 ments included four levels of temperature and 2-factor experiments  
 35 included two levels of temperature and three levels of light intensity  
 36 or initial copepod densities

1- Factor experiments			
Year	Duration (days)	Temperature	Light intensity (%)
2005–2007			
2005	91	$\Delta T = +6; +4; +2; +0$ °C	$I_0 = 16$
2006-1	38	$\Delta T = +6; +4; +2; +0$ °C	$I_0 = 100$
2006-2	68	$\Delta T = +6; +4; +2; +0$ °C	$I_0 = 64$
2007	81	$\Delta T = +6; +4; +2; +0$ °C	$I_0 = 32$
2-Factor experiments			
2008–2009			
2008	49	$\Delta T = +6; +0$ °C	$I_0 = 49; 57; 62\%$ Initial density of copepods (ind/L)
2009	38	$\Delta T = +6; +0$ °C	Cops = 1.5; 4; 10

Phytoplankton  $>5 \mu\text{m}$  were counted by inverted micros-  
 copy and distinguished at the genus level in most cases.  
 Small phytoplankton were counted by a flow cytometer  
 (FACScalibur, Becton Dickinson) and distinguished by  
 size and fluorescence of chlorophyll a and phycoerythrin.  
 Phytoplankton biomass was estimated as carbon calcu-  
 lated from cell volumes (Menden-Deuer & Lessard, 2000),  
 which was derived from linear measurements after  
 approximation to the nearest geometric standard solid  
 (for details about the calculation of phytoplankton bio-  
 mass, see Sommer & Lewandowska, 2011 and literature  
 cited therein). Primary production data were available to  
 us between 2007 (18 data points altogether, with more  
 frequent data during the first half of the experiment) and  
 2008–2009 (sampled every second working day) and was  
 calculated from  $^{14}\text{C}$ -bicarbonate uptake using samples  
 incubated inside the mesocosms at medium depth (data  
 for 2007: Breithaupt, 2009; data for 2008–2009: Lew-  
 andowska, 2011).

#### Data analysis

Based on the feeding preferences of the dominant grazers  
 (large ciliates and copepods), phytoplankton was divided  
 into two functional groups: edible (diatoms and filamen-  
 tous species  $500\text{--}1000 < \mu\text{m}^3$  cell volume, except for  
 several large species, see below) and less edible forms  
 (Sommer & Sommer, 2006). The latter was subdivided  
 into two groups, less edible small algae (autotrophic  
 picoplankton, nanoplankton  $<500\text{--}1000 \mu\text{m}^3$  cell volume)  
 and less edible large algae (including the big diatoms  
*Coscinodiscus* sp., *Rhizosolenia setigera* and the dinoflagel-  
 lates *Ceratium fusus* and *Ceratium tripos*).

We studied predictability by quantifying the difference  
 between paired mesocosms and all mesocosms within a  
 year and its change in time at various hierarchical levels.  
 Besides the difference in the biomass of total phytoplank-  
 ton, we examined the difference in the biomasses of the  
 three functional groups and of the taxonomic-functional  
 group autotrophic picoplankton (flow cytometric types  
 not matched to species,  $1\text{--}30 \mu\text{m}^3$ , Sommer & Lew-  
 andowska, 2011) and several phytoplankton species. The  
 latter were chosen because they were present in sufficient  
 abundances for extended periods of time in most of the  
 years and span a large size range: *Rhizosolenia alata* (cell  
 volume:  $37\text{--}700 \mu\text{m}^3$ ), *Thalassionema nitzschioides*  
 ( $1800 \mu\text{m}^3$ ), *Chaetoceros curvisetus* ( $1500 \mu\text{m}^3$ ), *Heterocapsa*  
*rotundata* ( $430 \mu\text{m}^3$ ) and *Skeletonema costatum* ( $283 \mu\text{m}^3$ ).  
 We also conducted the same analysis on the P/B ratio. We  
 performed a  $\log_2$  transformation on biomass and P/B data  
 to insure equal weight to all sampling dates regardless of



1 the absolute values on each date and ignored dates with  
2 zero biomass in at least one of the replicates.

3 We calculated divergence  $V_t$ , that is, the change of the  
4 difference with respect to time, according to the following  
5 equation:

$$6 \quad V_t = |x_{t,1} - x_{t,2}| - |x_{t-1,1} - x_{t-1,2}| \quad (1)$$

7  
8 where  $x_{t,1}$  and  $x_{t,2}$  are the  $\log_2$ -transformed values of  
9 biomass (of species, functional groups or communities) or  
10 P/B data in the compared mesocosms on date  $t$ . Values  $<0$   
11 indicate convergence, values  $>0$  divergence, and 0 indi-  
12 cates no change in difference. We only calculated the  
13 amount of divergence,  $V_t$ , between two successive sam-  
14 pling dates as the index is only informative about  
15 dynamics if calculated over short time-frames. For exam-  
16 ple, if mesocosm 1 has half the value of mesocosm 2 at  
17 time 1, but double the value of mesocosms 2 at time 2, this  
18 is a very strong change through time, but  $V_t$  remains zero  
19 as the amount of divergence that happened during this  
20 time is the same as the amount of convergence.

21 We quantified the mean difference ( $D$ ) in the  $\log_2$ -  
22 transformed values with the index:

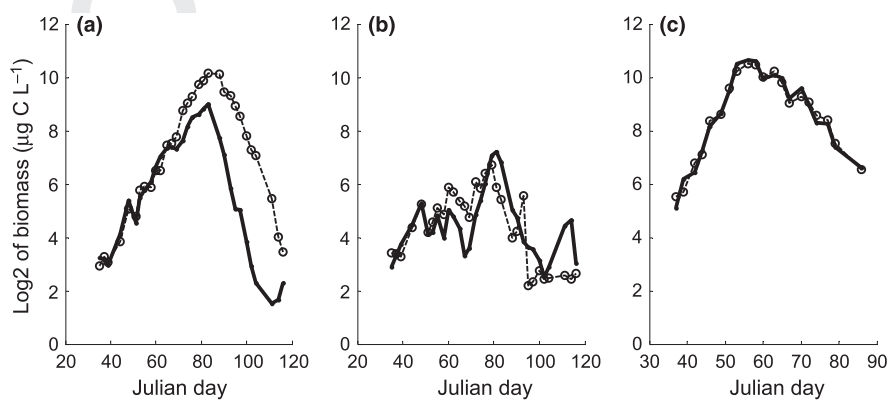
$$23 \quad D = \frac{\frac{1}{n} \cdot \sum_{t=1}^n |x_{t,1} - x_{t,2}|}{\frac{1}{3} \cdot \sum_{t=1}^3 |x_{t,1} - x_{t,2}|} \quad (2)$$

24  
25  
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28  
29 where  $n$  is the number of dates in a given year when  
30 phytoplankton samples or production measurements  
31 were available or, in the case of species, the number of  
32 sampling dates when the given species was found in both  
33 samples.

34 Values of  $D$  express the mean factorial difference  
35 between the biomasses or P/B of two mesocosms divided  
36 by their mean initial difference during the first three  
37

sampling dates, that is, the first week of the experiment.  
We took the mean of the first three sampling dates to  
reflect the fact that some cells counted just after filling are  
not alive and therefore do not contribute to the dynamics  
of the community later. The standardisation with the  
mean initial difference was necessary because the initial  
differences in species biomasses between the mesocosms  
were higher than for the functional groups and total  
community biomass. The index  $D$  is independent of the  
units and the magnitude of the variables because it is  
based on relative differences. This renders index  $D$   
suitable to compare hierarchical levels and periods within  
an experiment and among treatments.  $D$  is high if the  
average difference through time between two mesocosms  
is much higher than the initial difference, indicating  
prevalent divergence (Fig. 1a).  $D$  is close to 1 when the  
initial differences are maintained on average (memory  
effect), but are neither amplified nor buffered (Fig. 1b).  $D$   
is smaller than 1 when the biomasses in the two meso-  
cosms predominantly converge (Fig. 1c). This way,  $D$   
expresses our intuitive notion of 'unpredictability': sys-  
tems where small initial differences are amplified are  
unpredictable, and systems where they are maintained or  
buffered are predictable.

After calculating  $D$  for all replicates, the mean values  
were taken for further comparisons for all functional  
groups and species with the following exceptions: the  
values for *Heterocapsa rotundata*, *Rhizosolenia alata* and  
*Thalassionema nitzschioides* in 2005, two pairs of replicates  
in the case of *Chaetoceros curvicaetus* and *Rhizosolenia alata*,  
and all pairs in the case of *Thalassionema nitzschioides*  
in 2007. These were excluded from the calculations of  $D$   
for the species level owing to poor counting statistics result-  
ing from low abundances. The data from 2005 to 2007  
for the large less edible functional group were not analysed  
because of its extremely low abundances in these years.



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49  
50 **Fig. 1** Examples of pairs of replicates with (a) high ( $D = 8.35$ ), (b) intermediate ( $D = 2.26$ ) and (c) low ( $D = 0.43$ ) mean difference,  $D$ , calculated  
51 for the total phytoplankton biomass.

To test for differences in the mean  $D$  between the different functional groups and the P/B ratio, we conducted an ANOVA followed by a post hoc test (Tukey's HSD; Tukey, 1951), using the groups as fixed factors. We performed a similar analysis in the case of the species. We compared the grand mean of the  $D$  values of the functional groups and the grand mean of the  $D$  values of the species, assessing their difference with a  $t$ -test assuming unequal variances. Additionally, for each year, we calculated mean  $D$  of the total phytoplankton biomass and species and of the P/B ratio based on the difference among all mesocosms of the year. We compared the difference between the grand mean of  $D$  calculated this way to that calculated based on replicates between the phytoplankton and the species level with a  $t$ -test assuming unequal variances.

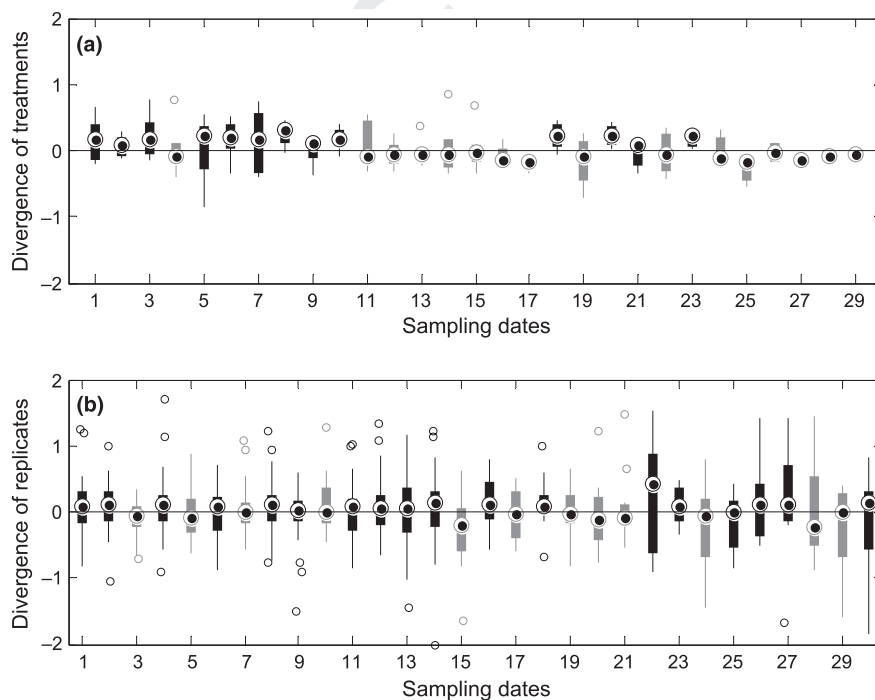
## Results

All mesocosms were similar in the general pattern of phytoplankton succession. In most of the mesocosms, the total phytoplankton biomass initially increased and it decreased after reaching its peak.

### Treatments vs. replicates

The divergence,  $V_t$  (i.e. the change of the difference), of the total biomass between any two mesocosms within 1 year showed a distinct pattern in time. Initially, it increased markedly but decreased during the second half of the experiments (Fig. 2a). In contrast,  $V_t$  values of the replicates calculated for the total biomass were variable over the experiments (Fig. 2b), which means that divergent and convergent dynamics occurred throughout the experiments between replicates. Occasionally extreme divergences were observed between two replicates, especially during the second half of the experiments, but we did not find any distinct relationship between their timing and the phase of phytoplankton succession.  $V_t$  values of the P/B between replicates and among treatments were also variable without any distinct temporal pattern.

As expected, the dynamics of biomasses and P/B ratios were more similar between replicates than among different treatments. The mean  $D$  of all years for total phytoplankton biomass calculated based on the difference between any mesocosm to any other mesocosm in the same year was 3.44 (standard deviation: 1.38), whereas the



**Fig. 2** Divergence,  $V_t$ , for total phytoplankton biomass for the sampling dates indicated on the  $x$ -axis among mesocosms of 1 year (i.e. partly different treatments) (a) and between replicates (b). As most of the experiments were conducted for <70 days (i.e. sampled <30 times), data from sampling dates >30 are not shown. Black boxes indicate dates when the median of  $V_t$  values for all pairs of mesocosms was above zero, indicating divergence on the given date compared to the previous date, while grey boxes indicate convergence. The central mark in each box is the median, the edges of the box are the 25th and 75th percentiles, the whiskers extend to the most extreme data points not considering outliers, and outliers are plotted individually.  $V_t$  calculated for species, functional groups and P/B ratios show a pattern similar to b).

1 mean  $D$  for total phytoplankton biomass of replicates was  
 2 2.26 (standard deviation: 1.58, Fig. 3a). The  $D$  values  
 3 calculated for species based on the differences of all  
 4 mesocosms ranged from 1.7 to 2.3 (with standard devi-  
 5 ations ranging from 0.8 to 1.8), similar to the range based  
 6 on the replicates (mean values: 1.5–2.2, standard devia-  
 7 tions: 0.9–3, Fig. 3b). Hence, the difference between  $D$   
 8 calculated for all mesocosms and for replicates was  
 9 significantly smaller at the species level than for the total  
 10 phytoplankton ( $t$ -test,  $t = 2.39$ , d.f. = 27,  $P < 0.05$ ). This  
 11 seems to suggest that the treatments had less effect at the  
 12 species than at the community level. However, the index  
 13  $D$  is normalised with the initial differences, which were  
 14 larger for species biomasses than for total phytoplankton  
 15 biomass. This implies that it was harder to detect an effect  
 16 of the treatments for the species than for the total  
 17 phytoplankton biomass.

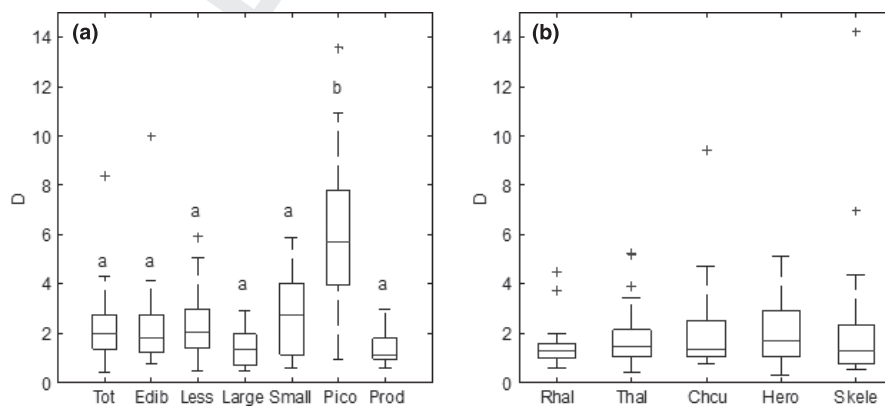
18 Mean  $D$  of P/B based on replicates was 1.32 (standard  
 19 deviation: 0.6, Fig. 3a), very close to the value based on  
 20 the difference of all mesocosms, which was 1.16 (standard  
 21 deviation: 0.41). The second value being slightly smaller  
 22 than the first is counterintuitive and is a result of  
 23 normalising  $D$  with the mean difference of the first three  
 24 sampling dates (eqn 2), which was larger among all  
 25 mesocosms than between replicates. Nevertheless, with-  
 26 out normalisation, the two values still fall in the same  
 27 range: mean  $D$  of replicates was 0.72 (standard deviation:  
 28 0.2) and mean  $D$  of all mesocosms was 0.99 (standard  
 29 deviation: 0.14).

#### Divergence ( $V_t$ ) and mean difference ( $D$ ) at various hierarchical levels

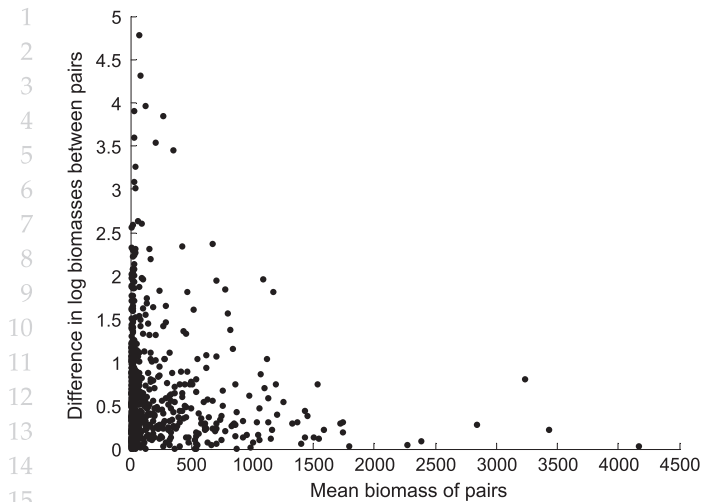
$V_t$  values calculated for the species and functional group biomasses were variable over time among all mesocosms and between the replicates (functional groups, between replicates: mean: 0.03, standard deviation: 0.64, among all mesocosms: mean: 0.07, std: 0.38; species, between replicates: mean: 0.04, std: 1.07, among all mesocosms: 0.14, std: 0.57), similarly to those calculated for the total phytoplankton biomass.

Except for picophytoplankton,  $D$  values of all the hierarchical levels studied were around two (median  $D$  values range: 1.1–2.72, Fig. 3); that is, on temporal average, the difference between the replicates was twice as much as during the first three sampling dates.

$D$  of the functional-taxonomic group picophytoplankton was significantly higher than  $D$  of the total phytoplankton, the functional groups and of the P/B ratio (Tukey's HSD,  $P < 0.05$ , Fig. 3a). There were no significant differences among the  $D$  values of the species (Fig. 3b, ANOVA,  $P > 0.6$ ). Similarly, there was no significant difference between the grand mean of  $D$  of the functional groups (picophytoplankton excluded) and of the species ( $t$ -test,  $t = 0.64$ , d.f. = 54,  $P > 0.5$ ). The mean  $D$  value of the P/B ratio was not significantly different from that of the biomass of the functional groups or species, but it varied only in a remarkably narrow range (Fig. 3a).



45 **Fig. 3** Difference index,  $D$  calculated between replicates 2005–2009 for (a) total phytoplankton biomass and P/B and biomass of functional  
 46 groups and (b) species biomass. The abbreviations mean: tot = total, edib = edible, totless = total less edible, small = small less edible, lar-  
 47 ge = large less edible phytoplankton, pico = picoplankton, prod = P/B, and Rhal = *Rhizosolenia alata*, Thal = *Thalassionema nitzschioides*,  
 48 Chcu = *Chaetoceros curvicaetus*, Hero = *Heterocapsa rotundata*, Skele = *Skeletonema costatum*. The letters 'a' and 'b' above the boxes in the left panel  
 49 indicate two significantly different groups after the Tukey's HSD test ( $\alpha < 0.05$ ). There were no significant differences in  $D$  among species (b). The  
 50 central mark on each box is the median, the edges of the box are the 25th and 75th percentiles and the whiskers extend to the most extreme data  
 51 points not considering outliers. The crosses indicate outliers. For the sake of better visualisation, one outlier was omitted: a  $D$  value of 24.3 for  
 52 picophytoplankton.



**Fig. 4** The relationship between the absolute difference in the log<sub>2</sub>-transformed biomasses of the mesocosm pairs  $|x_1 - x_2|$  and the mean total phytoplankton biomass of the mesocosm pairs on individual sampling dates. At high mean algal biomasses, differences between the two replicates were small, even in absolute values. At low mean biomasses, the replicates could be either similar or different.

#### *A mechanism of convergence: negative density dependence as a regulating factor*

Comparing the difference in the log-transformed total phytoplankton biomasses of the two replicates on a given date with their mean total phytoplankton biomass shows that differences between replicates were very low ( $<1$ ) during periods with high biomass (1500–4500  $\mu\text{g C L}^{-1}$ , Fig. 4). In contrast, during periods with lower biomasses, the difference values between the two replicates ranged from very small to a factor of 5 (Fig. 4). On dates with high biomass values, the maximum measured P/B ratios reached 0.04–0.54, which is a lower range than the maximum value during periods with lower biomasses, 2.04. This indicates bottom-up limitation when the biomass values were high.

#### **Discussion**

We analysed divergence ( $V$ ) and difference ( $D$ ), as indicators for predictability, of phytoplankton biomass and production between mesocosms to answer the question: How constrained and predictable do natural phytoplankton behave when influenced by complex food web interactions and realistic abiotic forcing?

Overall, even the most different treatments were similar in their general pattern, an increase in total biomass, driven by increasing light levels, and a decrease in biomass under nutrient depletion and severe grazing

pressure by herbivores, as also observed in field studies of spring phytoplankton (Sommer *et al.*, 1986). Nutrient depletion and grazing caused negative density dependence at the community level, which led to convergence in total biomass between replicates. In agreement with our first hypothesis, we observed a trend that the treatments within 1 year differed from each other more than the replicates in the case of the total phytoplankton. This was mostly due to strong divergences among the treatments in the exponential growth phase (Fig. 2a). During this period, phytoplankton dynamics were sensitive to light levels and grazing intensity, which depended on temperature in addition to grazer biomasses. Available light levels were the same in all mesocosms of 1 year (2005–2007, 2009) or varied only slightly (2008). Thus, the mesocosms of 1 year primarily differed in grazing intensity as they were either subjected to different temperature treatments (2005–2008) or contained different initial copepod densities (2009). Thus, the divergence of community biomass among treatments in the first half of the experiments was probably due to differences in grazing intensity. This assumption is supported by the lack of divergence in P/B in the first of the experiments and a very similar  $D$  of P/B among all mesocosms of 1 year to that of the replicates. Grazing presumably promoted divergence of community biomass among the mesocosms more strongly than divergence of P/B. During and after the phytoplankton bloom, the mesocosms converged, indicating a stronger role of nutrient limitation in phytoplankton dynamics, which was similar among all mesocosms within 1 year. At the species level,  $D$  of all mesocosms of 1 year was similar to that of the replicates. This indicates that individual species were probably similarly affected by the initial phytoplankton species composition (which was similar in all mesocosms in 1 year) than by forcing, which differed among the treatments. However, this pattern was also partly due to the methodology used here (see relevant section of Results).

In contrast to our second hypothesis, predictability at the species, group and community level was similar.  $D$  of the replicates was around two for most hierarchical levels (Fig. 3). This value means an amplification of initial differences in biomass merely by a factor of two. This shows that even the most divergent replicates remained fairly similar. The similarity indicates that the spring dynamics of phytoplankton are predictable if the abiotic and biotic forcing factors are known. This agrees with the relatively high goodness of fit between data and models under strong abiotic forcing (e.g. Peeters *et al.*, 2007; Tirok & Gaedke, 2007). Only the taxonomic-functional group



1 picophytoplankton had a significantly higher  $D$  than the  
 2 other hierarchical levels (Fig. 3a). This was because of  
 3 their typically very low  $D$  values on the first three dates.  
 4 This means that the initial abundances of the picophyto-  
 5 plankton in the replicates were more similar to each other  
 6 than those of the total phytoplankton or the functional  
 7 groups, which tended to differ more between the two  
 8 replicates. This was either the consequence of their more  
 9 even distribution in the water column or of the counting  
 10 method, which was different from that of the larger algae  
 11 (flow cytometry instead of inverted microscopy, see  
 12 Methods).

13 There was no substantial and monotonous increase in  
 14  $V_t$  either at the group (Fig. 2b) or at the species level,  
 15 which would be expected, for example, in the case of  
 16 systems with intrinsically chaotic dynamics (Hastings &  
 17 Powell, 1991). Although sometimes large  $V_t$  values arose,  
 18 especially at the species level, this was counterbalanced  
 19 by 'reset' periods, where the replicates converged (*sensu*  
 20 Grover & Lawton, 1994). This finding is in contrast to the  
 21 results of Beninca *et al.* (2008) who suggested that the  
 22 maximum time-frame for species-level predictions is 15–  
 23 30 days. The experiments analysed in their study were  
 24 run without directional forcing; thus, biotic interactions  
 25 had a larger role than in our system, which might explain  
 26 the lower predictability observed in their study. The  
 27 implication of this pattern for modellers is that, from the  
 28 viewpoint of predictability, aggregation of smaller units  
 29 into larger groups is neither discouraged nor encouraged.

30 In accordance with our third hypothesis, convergence  
 31 occurred at high community biomass (Fig. 4) presumably  
 32 close to the carrying capacity (indicated by nutrient  
 33 depletion, data not shown). The two replicates had similar  
 34 nutrient concentrations, and they were run under the  
 35 same light regimes. Thus, negative density dependence  
 36 caused by nutrient depletion and, to a minor extent, self-  
 37 shading was a mechanism that acted in both replicates  
 38 when they reached high biomasses. If one of the replicates  
 39 was approaching a high biomass faster than the other one,  
 40 nutrient depletion slowed it down. This caused conver-  
 41 gence of the mesocosms despite their potential differences  
 42 in initial species composition. In nature, pronounced  
 43 blooms and winter might serve as a general reset in terms  
 44 of total biomass, but less for species composition (Dakos  
 45 *et al.*, 2009), and even less for organisms forming resting  
 46 eggs and cysts. Another mechanism of community regu-  
 47 lation is the numerical response of grazers. As a result of  
 48 the short generation times of protozoans, they are espe-  
 49 cially likely to quickly track changes in phytoplankton  
 50 biomass. Predator effects have been shown to be able to  
 51 overrule the role of other interspecific interactions and

historical effects (Morin, 1984). On the other hand, the  
 occasionally large values of  $V_t$  over short time scales  
 observed in our study indicated the presence of positive  
 feedbacks, which caused a runaway of biomass in one of  
 the replicates. This warns against using distinct time  
 points of transients for generalisations about the analysis  
 of community dynamics and calls for longer community  
 observations.

Supporting hypothesis four, the predictability of the  
 P/B ratio was similar to that of total community biomass  
 (Fig. 3a). This indicates that mechanisms buffering as well  
 as amplifying initial small differences were present, which  
 prevented a lasting convergence or divergence.

Our study opens a new perspective on spring phyto-  
 plankton development; with the use of divergence and  
 difference indices, we gained insight into the relevant  
 factors affecting the predictability of phytoplankton bio-  
 mass at different hierarchical levels. This method could be  
 applied over a range of systems and trophic levels, to  
 enable more quantitative insights into the predictability of  
 communities and the expected reliability of forecast  
 models.

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