Vol. 473: 67–77, 2013
doi: 10.3354/meps10064

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 21

OPEN ACCESS

Initial dominance in coccolithophore communities affects community structure but does not translate into altered community functioning

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ABSTRACT: Climate change has the potential to profoundly influence the community structure and function of marine ecosystems. Prior to testing the consequences of altered environmental conditions on ecosystem functioning, it is first necessary to better understand how the functioning of an ecosystem is affected by its structure. Using phytoplankton communities with 4 naturally co-occurring coccolithophores including species of *Emiliania*, *Gephyrocapsa*, and *Calcidiscus* collected off the Azores, we experimentally tested whether varying initial dominance leads to different competitive outcomes and consequently affects community functioning, such as biomass and carbon accumulation. We manipulated initial community structure by creating 5 different dominance scenarios: (1) all species contributing evenly to total initial biomass, and (2–5) one of each species contributing 4× that of the remaining 3 species to total initial biomass. All 4 species were simultaneously grown in monocultures starting with the same total initial biomass as the communities. Monocultures differed significantly in total final biomass, particulate inorganic carbon, and particulate organic carbon content. Priority effects in the communities caused the initially dominant species to remain dominant during the stationary phase in 3 out of 4 cases. However, despite varying dominant species and different outcomes in the monocultures, community functioning was unaffected. We suggest that selective and facilitative effects are responsible for the equalization of community functioning. We conclude that monoculture experiments are not sufficient to predict whole-community responses, since species interactions can significantly alter the expected functional outcome.

KEY WORDS: Species interactions · Priority effect · Phytoplankton · Facilitation · Ecosystem functioning · Coccolithophores · *Emiliania huxleyi* · Global change

INTRODUCTION

Shifts in biodiversity due to major anthropogenic stressors, such as climate change, modifications of global biogeochemical cycles, and alteration of species composition in food webs, are significant and growing (Millennium Ecosystem Assessment 2005). In most ecosystems, not only is the number of species changing, but also their relative abundance and thereby dominance or evenness (Hillebrand et al. 2008). A meta-analysis of experimental studies by Walker et al. (2006) showed that warming increased dominance in plant communities within the tundra biome. Stachowicz et al. (2002) found a dominance shift to nonindigenous species due to warming in aquatic communities. Increasing CO_2 concentrations have also been found to alter dominance in grasslands (Niklaus et al. 2001). Changes in environmental conditions, such as pCO_2 and temperature in the oceans, have likewise induced dominance shifts in phytoplankton communities (Hare et al. 2007). Such alterations of biodiversity via changing species distri-

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butions most likely affect ecosystem functioning (i.e. biomass production, nutrient cycling, and habitat provision; Loreau et al. 2001, Hooper 2005). Whereas the effects of species loss on ecosystem processes have received broad attention (Hooper 2005, Cardinale et al. 2006, Hooper et al. 2012), the consequences of altered species dominance for emergent properties of communities and ecosystems are poorly investigated (Hillebrand et al. 2008). Evenness often changes more rapidly in response to anthropogenic stressors or altered environmental conditions than species richness. As such, altered patterns of evenness might lead to rapid changes in ecosystem functions before species are actually driven to extinction (Chapin et al. 2000).

Understanding the underlying mechanisms of ecosystem functioning is important from 2 perspectives: first, for better understanding of ecological theory in order to classify, interpret, and predict the world around us; and second, for the development of solutions to environmental issues, such as mitigating negative effects of carbon emissions (Heimann & Reichstein 2008). However, it remains challenging to resolve the effects of altered community structure on ecosystem functioning because consequences are often idiosyncratic and difficult to predict (Heimann & Reichstein 2008).

In nature, priority effects can have major ramifications on community development (Young et al. 2001, Fukami et al. 2005) but have been rarely studied. They occur when the first colonizer of a new habitat gains a numerical advantage such that it can exclude later colonists by monopolizing shared resources. Fukami et al. (2010) demonstrated the necessity of taking historical perspectives of community assembly into account when testing for the effects of community structure on ecosystem functioning. Their results showed that even a small initial assembly effect on community structure can result in large variations in ecosystem functioning if the compositional difference is due to one or a few functionally important species dominating different communities. Alternatively, community assembly may be important to community structure, but not to ecosystem functioning if variation in initial community assembly results in compositionally divergent, but functionally convergent, community structure.

Observed responses of ecosystem processes to changes in community structure or diversity can be broadly grouped into 2 types (Loreau & Hector 2001). First, the complementarity effect, which posits that resource partitioning or positive interactions in a community lead to increased total resource use. In particular, niche differentiation or facilitation between species can increase the performance of communities above that expected from the best performing monoculture (referred to as transgressive overyielding). Second, the selection effect posits that the relationship between biodiversity and ecosystem functioning is determined by selective processes, such as interspecific competition, which cause the dominance of one very effective species driving ecosystem functioning. However, community overyielding due to selection effects never exceeds the performance of the best performing monoculture, but rather the performance of the average monoculture (Loreau & Hector 2001).

In the present study, we used a model system of 4 marine, unicellular, calcifying phytoplankton species (coccolithophores) to experimentally test whether varying initial dominance scenarios translate into altered community functioning. Coccolithophores are distinguished by calcium carbonate plates referred to as coccoliths. Due to their worldwide distribution and their important contribution to carbon fixation, coccolithophores play a key role in global biogeochemical cycles (Sikes & Fabry 1994). In particular, *Emiliania huxleyi* has the capacity to form extensive blooms in both coastal and oceanic waters (Brown & Yoder 1994) when water conditions are favorable. *E. huxleyi* blooms have been recorded to achieve cell concentrations of up to 115 million cells l^{-1} (Berge 1962). However, the particular set of conditions that leads to these blooms is not fully understood. Bottom-up factors (shallow mixed layer, high light, and high N:P ratios) and top-down factors (reduced grazing) have all been implicated as important for the development of *E. huxleyi* blooms (Tyrrell & Merico 2004).

In this study, we explored biomass and carbon accumulation of the 4 species in monocultures and how their performance is reflected in communities with different initial dominance scenarios. In particular, we tested the following hypotheses: (1) in monocultures, species differ in their carrying capacities. In particular, *Emiliania huxleyi* was expected to show the highest carrying capacity, which corresponds to massive blooms occurring in nature. (2) In communities, varying initial dominance scenarios affect the competitive outcome and consequently community structure. More precisely, the initially dominant species is also expected to retain its dominance due to priority effects. (3) Community functioning depends on community structure. In particular, we expected communities dominated by *E. huxleyi* to possess the highest carrying capacities due to selection effects.

MATERIALS AND METHODS

Study organisms

Four naturally co-occurring coccolithophore species, i.e. *Gephyrocapsa oceanica* (A), *G. muellerae* (B), *Calcidiscus quadriperforatus* (C), and *Emiliania huxleyi* (D) were used in the experiment. Cultures originated from strains that were isolated in April 2010 from waters off Faial Island (Azores, North Atlantic). The average cell biovolume of the 4 species was clearly different. Biovolumes were based on the spherical shape of the cells as described by Hillebrand et al. (1999), and calculated by determining the diameters for each species with a Z2™ COULTER COUNTER® prior to the experiment. The measured diameters resulted in a volume of 91 μm^3 for *E. huxleyi*, 99 μm^3 for *G. muellerae*, 205 μm^3 for *G. oceanica*, and 1920 μm^3 for *C. quadriperforatus*.

Experimental design

Initial community structure was manipulated by creating 5 different dominance scenarios (A dominant, B dominant, C dominant, D dominant, ABCD even). All 4 species were simultaneously grown in monocultures; this design allowed for quantitative comparisons between monocultures and communities. Each treatment was replicated 4 times resulting in 36 experimental units that comprised 2 l polycarbonate bottles randomly distributed across 4 climate cabinets.

At the onset of the experiment, 8 $\mu mol\ l^{-1}$ nitrate and 0.5 $\mu mol\ l^{-1}$ phosphate were added to 100 l of North Sea water with a salinity of 32 psu. These nutrient concentrations corresponded to a molar ratio of dissolved nitrogen to dissolved phosphate of 16:1. This reflects the prevailing oligotrophic nutrient regime across the study area that was measured while isolating the study organisms in April 2010. Vitamin and trace metal concentrations corresponded to 1/10 of a common f/2 medium (Guillard 1975). Initial pCO_2 and total alkalinity represented 380 ppm and 2330 $\mu mol\ kg^{-1}$, respectively. After sterile filtration (0.2 µm pore size), the water was transferred into the experimental units.

The differences in cell biovolume among the 4 species were balanced by starting each treatment with the same total initial biovolume, corresponding to a total initial biomass, of 153 600 $\mu m^3\ ml^{-1}$. Following field observations of phytoplankton community structure before the onset of a spring bloom (S. Jaschinski pers. comm.), dominance of species in the respective treatments was manipulated by adding the desired dominant species in a 4× higher concentration than the other 3 remaining species. In the even treatment, each species contributed 25% to total initial biomass.

Cultures were exposed to 16°C and a light intensity of 130 $\mu mol\ m^{-2}\ s^{-1}$ following a 16:8 h light:dark cycle. In order to limit sedimentation during the experiment, bottles were carefully rotated 3 times a day, each time with 15 rotations. The experimental duration was between 9 and 15 d. To ensure that cultures were sampled at the same state of growth, the exact development of each culture was determined by a sigmoidal growth model (see below).

Sampling and response variables

Cell abundance (n) and size (d) were determined every day with a Z2™ COULTER COUNTER®. The decision to terminate a culture was based on a statistically significant fit to the growth model:

$$n_t = a \times \{1 + [(a - b)/b] \times e^{(-\mu \times t)}\}^{-1} \quad (1)$$

where n_t is the number of cells after t days, a is the maximum cell abundance (carrying capacity), b is the starting cell number, and µ is the growth rate. The first day on which the growth curve of a culture significantly fitted the model, i.e. reached the stationary phase (carrying capacity), where outcome of interspecific competition is mostly pronounced, was defined as the first of 3 d in the stationary phase, after which the cultures were terminated. Final cell abundance and cell size were used to calculate total biovolume ($= n \times 1/6 \times \pi \times d^3$) after Hillebrand et al. (1999) as a measure of total biomass.

Community composition was determined every day by scanning electron microscopy (SEM) using a Phenom G2 pure desktop SEM. Samples were filtered through Whatman Nuclepore™ track-etched polycarbonate membranes (0.8 µm pore size, 25 mm Ø), dried, and analyzed. In total, 1000 cells $sample^{-1}$ were identified to calculate the relative abundance of each species. Additionally, the diameters of 25 randomly chosen cells per species were measured and used to calculate the average cell biovolume of each species. Cell abundance, relative abundance of each species, and the corresponding cell biovolume were used to calculate absolute biomass of each contributing species in the communities.

At the end of the experiment, samples for dissolved inorganic nutrients, total particulate carbon (TPC),

and particulate organic carbon (POC) were taken (Whatman GF/F filters, 25 mm Ø). For the latter, the particulate inorganic carbon (PIC) was removed by exposing filters containing TPC to fuming hydrochloric acid for 12 h. Before measurement, filters were dried at 60°C, folded, packed in tin cups, and subsequently analyzed with an elemental analyzer with a thermal conductivity detector (FlashEA 1112). PIC was determined by subtracting POC from TPC. Discriminating between POC and PIC allows disentanglement of the proportions of biologically fixed carbon that either return back to the carbon cycle through remineralization and/or decomposition (POC) or contribute to carbon export from the surface to the ocean sediments (PIC). Dissolved inorganic phosphate and nitrate were measured with continuous flow analyses following Hansen & Koroleff (1999) using a SKALAR SAN^{PLUS} auto-analyzer system.

Statistical analyses

Prior to statistical analyses, data were tested for normality and homogeneity of variances. If data were not normally distributed or variances were not homogeneous, data were square-root transformed. Addressing hypothesis 1, we tested the effect of species identity (SI) on total biomass, TPC, POC, and PIC by calculating a 1-way analysis of variance (ANOVA) among the monocultures (4 levels). To determine which species significantly differed from each other, all possible pairs of means were compared by Tukey's HSD test afterwards.

In addition, the final absolute biomass of the initially dominant species within each of the different communities, excluding the even treatment, was tested against the yield of the respective monoculture with a Student's *t*-test (i.e. A in Abcd versus A in monoculture, etc.).

Addressing hypothesis 3, we tested the effects of initial community structure (ICS) on total biomass, TPC, POC, and PIC by calculating a 1-way ANOVA among the communities with 5 levels of dominance. The occurrence of overyielding due to selection effects was tested by calculating a 1-way ANOVA with 6 levels including the average monoculture in addition to the 5 different communities. To determine which communities significantly differed from the average monoculture, each of the dominance scenarios was compared to the average monoculture by Fisher's protected LSD test afterwards.

The consistency of TPC, POC, and PIC with total biomass was confirmed by a positive Pearson correlation coefficient in both the monocultures and the communities (monocultures: $r_{TPC} = 0.89$, $r_{POC} = 0.92$, $r_{PIC} = 0.74$, $p < 0.01$ for all, $N = 16$; communities: $r_{TPC} = 0.86$, $r_{POC} = 0.77$, $r_{PIC} = 0.89$, $p < 0.01$ for all, $N = 20$). Therefore, we consider biomass as the appropriate response variable to mechanistically explain our findings.

Observed differences in the duration until nutrient depletion between the communities and their respective monocultures (e.g. abcD versus D) were confirmed with a Student's *t*-test comparing the number of days that it took a culture to deplete nutrients.

RESULTS

Total yields of monocultures

Species identity significantly affected total biomass, TPC, and POC (Table 1, Fig. 1). The 4 species differed significantly in total biomass, except *Calcidiscus quadriperforatus* (C) from *Emiliania huxleyi* (D). *Gephyrocapsa oceanica* (A) was the best performing species (i.e. reached the significantly highest carrying capacity; Tukey HSD: A versus B, C, D: p <

Table 1. Results of 1-way ANOVAs testing the effects of species identity (SI) and initial community structure (ICS) on total biomass, total particulate carbon (TPC), total particulate organic carbon (POC), and particulate inorganic carbon (PIC) among monocultures (4 levels), among communities (5 levels), and among communities plus the average monoculture (6 levels). Shown are degrees of freedom (df_{model}, $df_{residual}$), the variance explained by the model (R^2), the *F* ratio, and the probability that the variation is random. Values in **bold** are significant at $p < 0.05$

	Monocultures					Communities					Communities plus average monoculture			
Response Variable	Factor	df	R^2	*F*	p	Factor	df	R^2	*F*	p	df	R^2	*F*	p
Total biomass	SI	3, 12	0.92	59.07	**<0.001**	ICS	4, 15	0.21	2.23	0.12	5, 30	0.26	3.47	**<0.05**
TPC	SI	3, 12	0.60	8.48	**<0.01**	ICS	4, 15	0.02	1.08	0.40	5, 30	0.00	1.01	0.43
POC	SI	3, 12	0.86	32.56	**<0.001**	ICS	4, 15	0.18	2.02	0.14	5, 30	0.07	1.53	0.21
PIC	SI	3, 12	0.24	2.62	0.10	ICS	4, 15	0.06	0.74	0.58	5, 30	–0.06	0.59	0.71

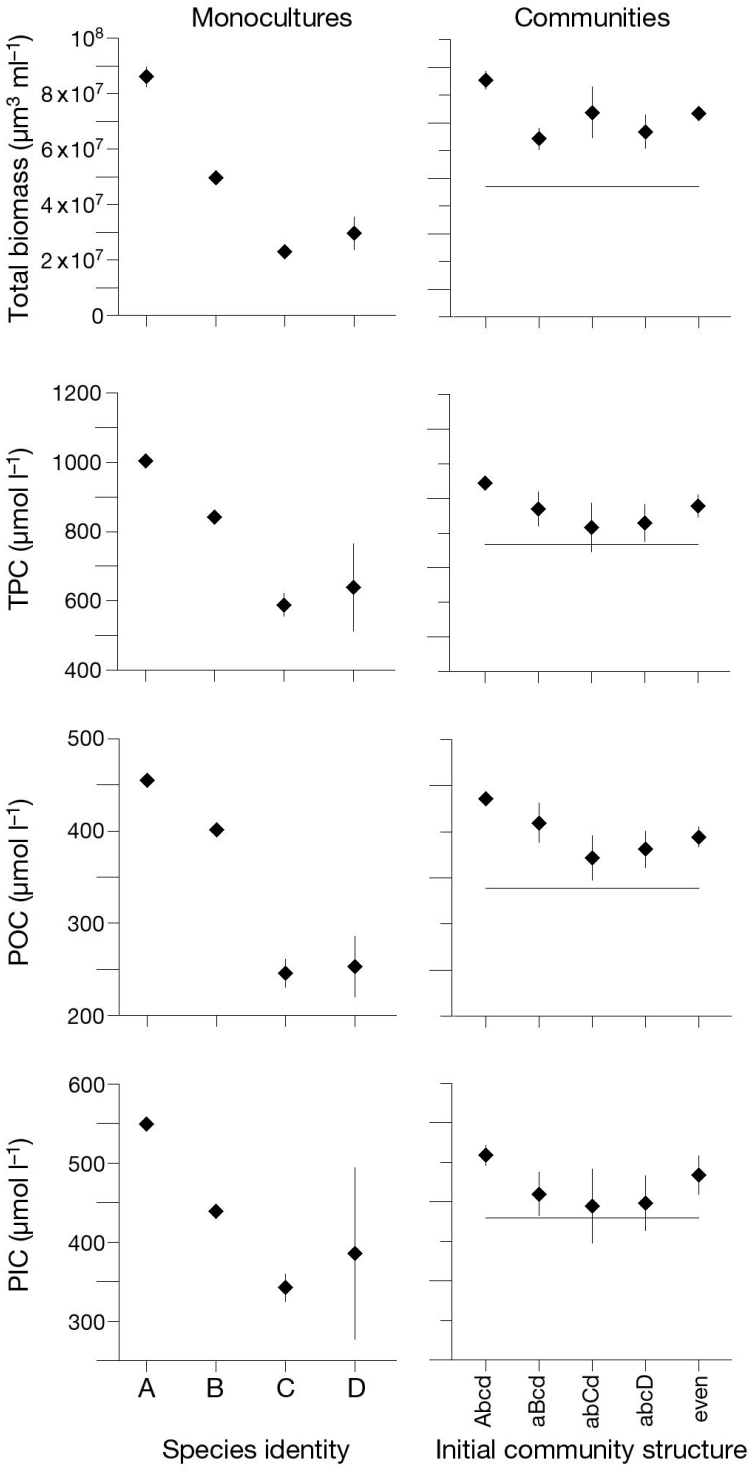

Fig. 1. Total biomass (calculated as biovolume), total particulate carbon (TPC), particulate organic carbon (POC), and particulate inorganic carbon (PIC) in monocultures and communities at the end of the experiment. Capital letters on the *x*-axes of the community plots indicate the initial dominant species. Species identities are (A) *Gephyrocapsa oceanica*, (B) *G. muellerae*, (C) *Calcidiscus quadriperforatus* and (D) *Emiliania huxleyi*. Black lines refer to the overall mean of the average monoculture. Error bars are ± SE

0.001). The second highest yielding species was *G. muellerae* (B; Tukey HSD: B versus C: $p < 0.001$; B versus D: $p < 0.05$; Fig. 1). *C. quadriperforatus* (C) and *E. huxleyi* (D) were both lower-yielding species (Fig. 1). Regarding TPC and POC accumulation, both *Gephyrocapsa* species (A,B) were significantly higher yielding than *C. quadriperforatus* (C) and *E. huxleyi* (D); (Tukey HSD: $p < 0.01$). PIC accumulation was not significantly affected by species identity (Table 1).

Final community structure

Analyses of the relative biomass of each species over time in the different communities showed that in the cases of *Gephyrocapsa oceanica* (A), *G. muellerae* (B), and *Emiliania huxleyi* (D) being the initially dominant species, these species remained dominant until stationary phase. Their final contributions to total biomass accounted for 57, 50, and 75%, respectively (Fig. 2). In the case of *Calcidiscus quadriperforatus* (C) being the initially dominant species and in the even treatment, *Emiliania huxleyi* (D) ultimately dominated these communities. Here, the relative contribution of *E. huxleyi* (D) to total biomass represented 40 and 48%, respectively (Fig. 2).

Comparing the final absolute biomass of the initially dominant species within each of the different communities with the biomass of its respective monoculture showed that the yields of all species except *Emiliania huxleyi* (D) were significantly lower in the communities (Table 2, Fig. 3). The biomass of *E. huxleyi* in the community (abcD) was 1.7-fold higher compared to its respective monoculture (Fig. 3).

Total yields of communities

Initial dominance structure had no effect on community functioning; the communities with initially different dominance scenarios were not signifi-

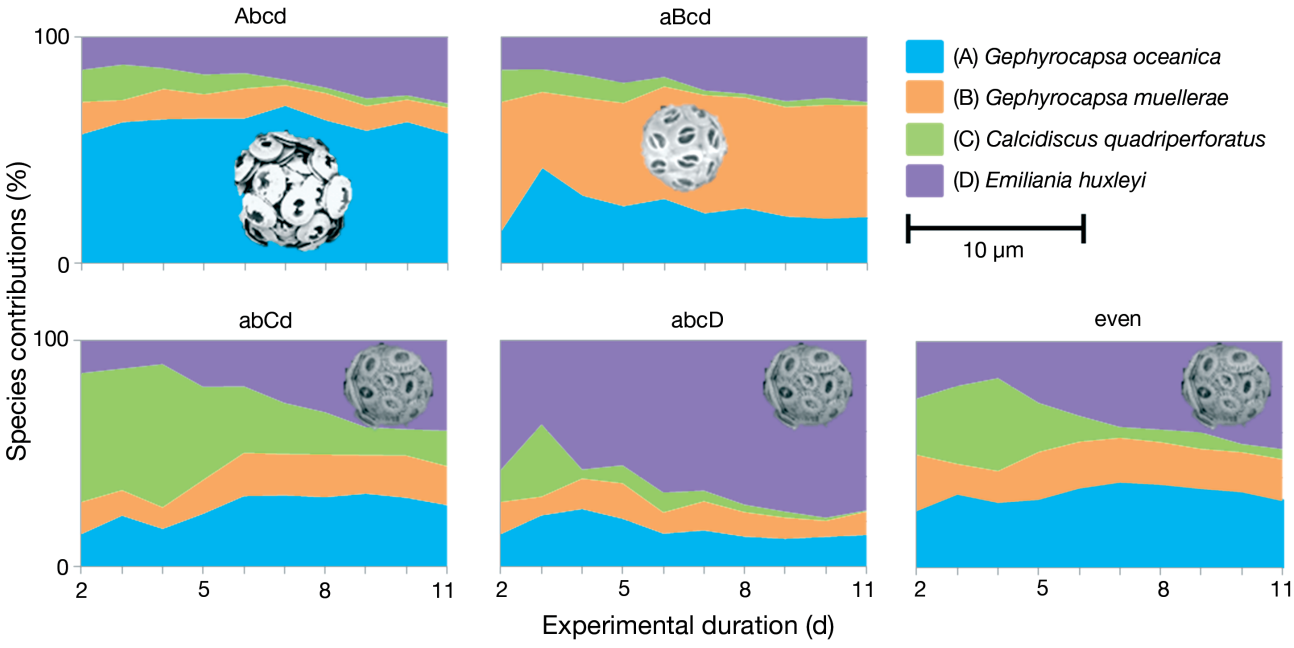

Fig. 2. Relative community compositions over time in the different communities (capital letters in the headings indicate the initial dominant species, and scanning electron micrographs illustrate the dominant species at the end of the experiment)

Table 2. Results of Student's *t*-tests comparing the final biomass of the initially dominant species (capital letters: A = *Gephyrocapsa oceanica*, B = *G. muellerae*, C = *Calcidiscus quadriperforatus*, D = *Emiliania huxleyi*) within each of the different communities, excluding the even treatment, with the yield of the respective monoculture. Shown are degrees of freedom (df), the *t* value, and the probability that the variation is random. Values in **bold** are significant at $p < 0.05$

Test	df	*t*	p
A in Abcd vs. A in monoculture	3	–7.95	**<0.001**
B in aBcd vs. B in monoculture	3	–8.66	**<0.001**
C in abCd vs. C in monoculture	3	–3.38	**<0.05**
D in abcD vs. D in monoculture	3	2.85	**<0.05**

cantly dissimilar from each other in terms of total biomass, TPC, POC, and PIC (Table 1, Fig. 1). Comparing the performance of each community with the average monoculture revealed that all communities were in general higher yielding in terms of biomass but not in terms of TPC, POC, and PIC (Table 1). The communities that were initially dominated by *Gephyrocapsa oceanica* (A; Fisher's protected LSD test: $p < 0.01$) and *Calcidiscus quadriperforatus* (C; Fisher's protected LSD test: $p < 0.05$) as well as the initially even communities (Fisher's protected LSD test: $p < 0.05$) were significantly higher yielding than the average monoculture. The communities that were initially dominated by *G. muellerae* (B) and *Emiliania huxleyi* (D) were both marginally higher than the average monoculture (Fisher's protected LSD test: $p = 0.091$ and 0.063, respectively).

Dissolved inorganic nitrogen and phosphorus

The amount of phosphorus taken up was similar in all communities and was depleted after 11 d (Fig. 4). The monocultures of *Gephyrocapsa oceanica* (A), *G. muellerae* (B), and *Calcidiscus quadriperforatus* (C) followed the same pattern. *Emiliania huxleyi* (D) in monoculture showed the highest affinity for inorganic phosphorus compared to the other 3 species, leading to fastest depletion after 8 d (Fig. 4). Thus, in the communities which were initially dominated by *E. huxleyi* (abcD), inorganic phosphorus was available significantly longer (on average 2 d) than in the *E. huxleyi* (D) monocultures (*t*-test: df = 6, $t = –3.0$, $p < 0.05$; Fig. 4).

Nitrogen was taken up similarly in all the communities and depleted after 8 d except in the community that was initially dominated by *Emiliania huxleyi* (D), where nitrogen was available until Day 10 (Fig. 4). The depletion of nitrogen followed the same pattern in the monocultures except the monoculture of *Calcidiscus quadriperforatus* (C). Here, nitrogen was available until Day 14.

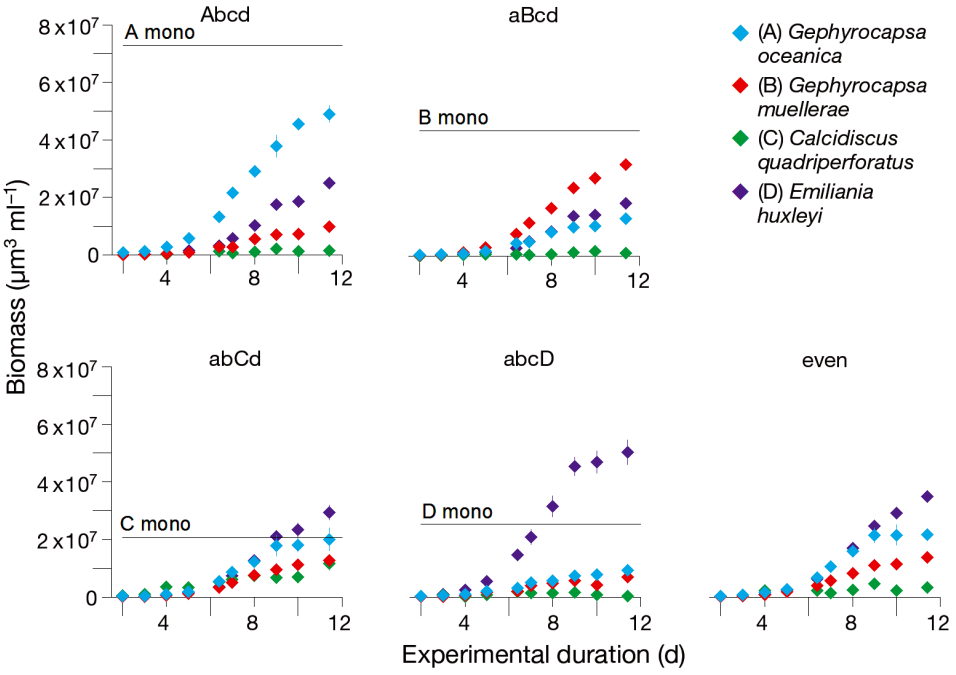

Fig. 3. Absolute biomass (calculated as biovolume) of each species in the different communities (capital letters in the headings indicate the initial dominant species). Black lines refer to the mean of the dominant species in monocultures (mono) at the end of the experiment. Error bars are ± SE

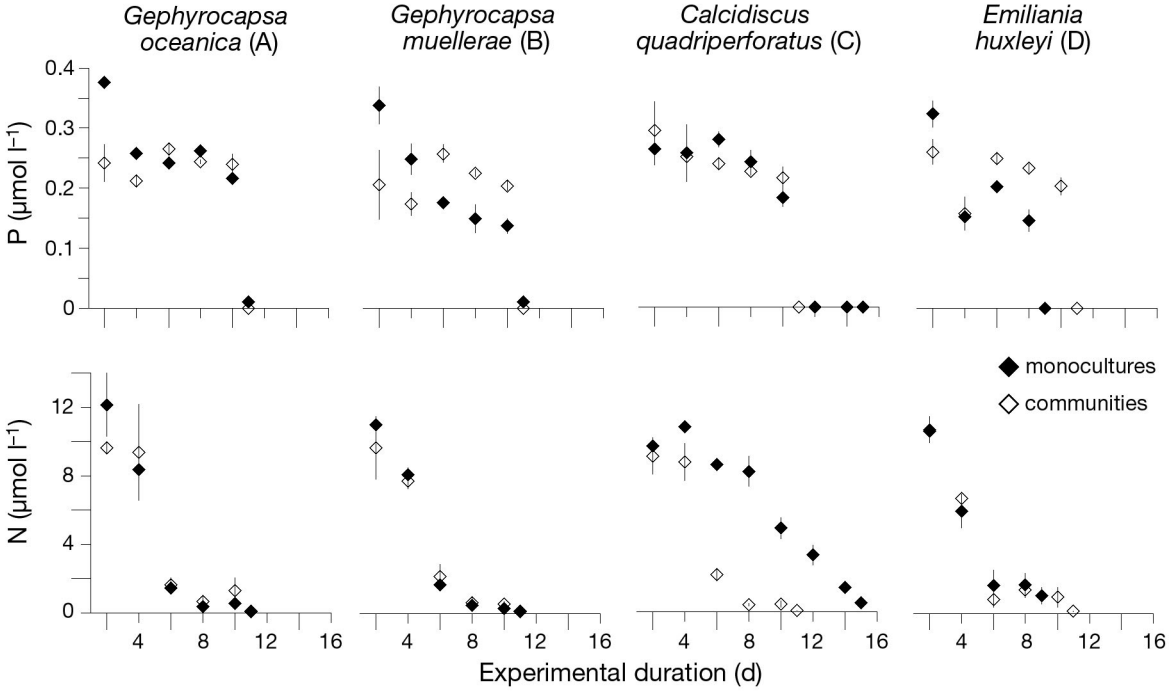

Fig. 4. Total dissolved inorganic phosphorus (P) and nitrogen (N) over time in the different monocultures and communities. Headings indicate the species (in monoculture) and the initial dominant species (in the community). The quantification limit is 0.1 µmol l^{-1} and indicates the minimum concentration at which we can be confident that the numerical result is accurate. Data below the quantification limit are assumed to be 0

DISCUSSION

The 4 species clearly differed in their carrying capacities as demonstrated in the monocultures (supporting hypothesis 1). However, contrary to our expectations, the highest carrying capacity was not established by *Emiliania huxleyi* but by *Gephyrocapsa oceanica*. In general, varying initial dominance scenarios in the communities led to different competitive outcomes that were consequently reflected in community structure (supporting hypothesis 2). More precisely, in 3 out of 4 cases, the initially dominant species (i.e. *G. oceanica*, *G. muellerae*, and *E. huxleyi*) remained dominant due to priority effects. However, these differences in community structure were not translated into community functioning (rejecting hypothesis 3), as could be expected according to different outcomes in the monocultures. That is, the overall performance of the communities was equal. In general, all communities overyielded the average monoculture in terms of biomass due to selective and facilitative effects.

Community structure and functioning

Prior to the onset of phytoplankton spring blooms, alongside a variety of environmental conditions, the initial composition and distribution of phytoplankton species is assumed to greatly influence the development of the blooms. In this study, we demonstrated that the community structure in the stationary phase indeed was strongly influenced by the initial community composition at the onset of growth. However, these differences in community structure were not translated into community functioning. This confirmed the suggestion by Fukami et al. (2005) that community assembly may be important to community structure, but not to its functioning if the variation in initial community assembly results in compositionally divergent, but functionally convergent, community structure. To date, demonstrations of priority effects have focused on temporal scales, where pre-emptive competition means that early-arriving species make resources unavailable to other, later-arriving species (Tilman 1988). Other forms of priority effects include predation (Holt & Polis 1997), environmental modification (Knowlton 2004) and, more recently, historical perspectives of evolutionary assembly through diversification (Fukami et al. 2007). However, initial community structure is still not fully taken into account when explaining the development of phytoplankton blooms. The initial community structure is no less important to the functioning, spatial extent, and duration of phytoplankton spring blooms than are the abiotic conditions.

In general, the functioning of the present communities was shaped by selective and partly by facilitative processes. That is, functioning in all communities was driven by single effective species, resulting in total community performances overyielding the average monoculture. Moreover, our results suggest that different mechanisms were responsible for equalizing the functioning among the communities despite distinct expectations from the monocultures and explicit differences in community composition. In the case of *Gephyrocapsa oceanica* or *G. muellerae* being the dominant species, community functioning was driven only by classical selection effects. That is, the dominant competitor was the driving species for total community performance, and thus community functioning did not deviate from the respective dominant species' monoculture. In the communities that contained *Emiliania huxleyi* as initially dominant, its performance was facilitated by the presence of at least one of the other 3 species. The facilitation effect caused the *E. huxleyi*-dominated communities to clearly perform better than was expected from the *E. huxleyi* monocultures (Fig. 3). Consequently, the differences in structure among the communities leveled out in functioning. The experimental design used in the present study, however, did not allow us to determine which particular species or set of species was responsible for the facilitation effect.

Though highly speculative, a possible mechanistic explanation for the facilitative effect might be found in different phosphorus sources between the monocultures of *Emiliania huxleyi* and the communities which were initially dominated by *E. huxleyi*. Inorganic phosphorus was available significantly longer in the *E. huxleyi*-dominated communities compared to the respective monocultures, which suggests that *E. huxleyi* used an alternative phosphorus source such as organic phosphorus. This allowed for almost one more cell division, resulting in a higher population density of *E. huxleyi* than could be expected from its monocultures. *E. huxleyi* is known to be superior to other algal species under extremely phosphorus-limited conditions, which is reflected in massive *E. huxleyi* blooms in phosphorus-depleted areas or seasons (Egge & Heimdahl 1994, Tyrrell & Taylor 1996). This is caused by its high affinity for inorganic phosphorus on the one hand, and on the other by its possession of several alkaline phosphatase (APase) enzyme systems making organic

phosphorus available (Riegman et al. 2000, Xu et al. 2010), which is, for example, provided by degrading cells. For *E. huxleyi* it could be shown that relevant APases were induced and enzyme activity rapidly increased with phosphorus limitation (Riegman et al. 2000, Xu et al. 2010). So far, no expression of these APases could be detected in other phytoplankton species (Xu et al. 2010). APase activity can enhance population growth by up to 90% through organic phosphorus uptake depending on the concentration of available organic phosphorus. Moreover, in chemostat experiments, organic phosphorus uptake rate correlated negatively with growth rate and positively with organic phosphorus concentration (Riegman et al. 2000). This means that APase activity becomes increasingly important during the stationary phase (Xu et al. 2010), i.e. phytoplankton bloom peak, when more organic phosphorus is available through degrading cells. Interpreting this in the context of our study suggests that in the *E. huxleyi*-dominated communities, organic phosphorus was provided by degrading cells of the subdominant species. This source of organic phosphorus was not available in *E. huxleyi* monocultures and thus led first to faster depletion of inorganic phosphorus and second to significantly lower cell abundance. Strictly speaking, facilitation describes species interactions that benefit at least 1 of the participants and harm neither (Stachowicz 2001). Thus, our finding is not a true facilitation effect because the subdominant species experienced reduced performance. This is likely due to the general competitive advantage of *E. huxleyi* in both inorganic and organic phosphorus uptake. However, overyielding can be taken as an indicator for facilitation (Hector et al. 2009).

The communities that were initially dominated by *Calcidiscus quadriperforatus* or evenly assembled and were finally dominated by *Emiliania huxleyi* likewise did not differ from the other communities in total functioning and also overyielded the average monoculture. In both communities, final dominance of *E. huxleyi* was less pronounced compared to the communities that were initially dominated by *E. huxleyi* and the final contribution of each species was more even. However, in these communities, *E. huxleyi* was likewise never outperformed by its respective monoculture, suggesting that it benefitted from the presence of the other species via the suggested phosphorus uptake strategies. Thus, the dominance of *E. huxleyi* in the presence of subdominant species most likely led to an increased resource use efficiency along the altered N:P gradient. Overall, the different mechanisms that were triggered by relatively small compositional differences during community assembly led to communities that showed either lower or higher carrying capacities of their dominant species than could be expected from the corresponding monocultures. Thus, independent of their structure, the overall functioning in the communities equalized.

Implications for changing oceans

The anthropogenically induced rise in atmospheric pCO_2 leads to changes in seawater carbonate chemistry known as ocean acidification, which is considered to have major effects on calcifying organisms (Caldeira & Wickett 2005, Orr et al. 2005). In the present experiment, we used model organisms that were previously used to address hypotheses testing the consequences of rising atmospheric pCO_2 mostly for the physiological performance of these organisms (e.g. Riebesell et al. 2000, Langer et al. 2006). In this study, we focused on ecological mechanisms pointing to the fact that different interaction effects between species make functional outcomes hard to predict. Therefore, multifactorial approaches combining community structure and environmental stress might have unexpected implications for population responses to global climate change. This has the potential to produce more realistic results than derived from pure monoculture experiments.

Dissolution of CO_2 in seawater results in increased concentrations of bicarbonate and hydrogen ions and therefore a decrease in seawater pH. This eventually leads to a decreasing availability of carbonate ions. Since the latter are crucial building blocks in calcifying organisms, a rising atmospheric pCO_2 potentially leads to reduced calcification in marine organisms (Guinotte & Fabry 2008). Following physical laws, the solubility of CO_2 increases with decreasing temperature. Thus, calcifying organisms might primarily become impaired or even lost during the overwintering phase in temperate and polar latitudes. This might have severe consequences for spring bloom community compositions and consequent community functioning.

Previous studies have demonstrated that among calcifying phytoplankton there are species-specific differences in the response to changes in seawater carbonate chemistry. Among the coccolithophores, *Gephyrocapsa oceanica* (Langer et al. 2006) seems to be most prone to increasing pCO_2, whereas *Emiliania huxleyi* showed less sensitivity (Riebesell et al.

2000) or adaptive evolution in the long term (Lohbeck et al. 2012). Our results point to the fact that *E. huxleyi* may depend on other subdominant coccolithophore species to facilitate its performance and consequently allow the occurrence of massive *E. huxleyi* blooms. Assuming that *G. oceanica* would be responsible for the facilitative effect in our model system, losing this species due to direct negative physiological effects on changes in seawater carbonate chemistry would consequently lead to indirect negative effects of altered community structure on the performance of *E. huxleyi*. However, transferring this to natural communities and further disentangling the effects of community structure and abiotic stress such as rising pCO_2 requires the inclusion of more functional groups such as diatoms. The latter have been shown to initially dominate natural phytoplankton spring blooms until dissolved inorganic nutrients, primarily silicate and phosphorus, become limiting (Tyrrell & Merico 2004). Subsequent blooms of *E. huxleyi* are among other environmental factors triggered by low dissolved inorganic phosphorus concentrations and increased availability of dissolved organic phosphorus due to degrading diatoms. The great challenge predicting the effects of climate change, such as increasing sea surface temperature and pCO_2, on ecosystems is in understanding how altered species interactions will affect succession and extent of phytoplankton blooms.

To our knowledge, this study is among the first to mechanistically show that small differences in initial community composition can have unpredictable effects on community functioning, as species interactions are highly idiosyncratic, which can significantly alter the functional outcome expected from monocultures. This points to the likelihood that understanding changing community interactions along with global environmental change such as ocean acidification will uncover unexpected consequences for biogeochemical cycles.

Acknowledgements. This study was financed by the Leibniz Competitive Fund within the Pact for Research and Innovation (SAW). We thank B. Gardeler, C. Meyer, and S. Krug for lab assistance; U. Sommer for very helpful comments; and D. Boyce and A. Paul for critically checking the written English.

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Editorial responsibility: Martin Solan, Southampton, UK

Submitted: November 28, 2011; September 18, 2012
Proofs received from author(s): January 7, 2013