WATER COLUMN STRATIFICATION, PHYTOPLANKTON DIVERSITY AND CONSEQUENCES FOR RESOURCE USE AND PRODUCTIVITY

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Stratification of water columns determines the general availability of light and nutrients for phytoplankton growth. However, seasonal stratification can be affected and disturbed by a-seasonal effects. Hence, disturbances of water column stratification imply disturbances for phytoplankton dynamics since it causes alterations in the relative supply of light and nutrients. According to ecological theory, the frequency of disturbance strongly affects the diversity of biological communities. Whether disturbances increase or decrease the diversity of a community depends on productivity and resource supply rate. However, this important interaction between disturbances and nutrient supply rate is seldom considered investigating effects of disturbance on plankton communities. Our experiments will result in a first data set showing how phytoplankton species diversity, resource use efficiency and carbon production are linked within stratification disturbance in a marine phytoplankton community and how ciliates and zooplankton communities are influenced by these stratification disturbances.

1. INTRODUCTION

The seasonal stratification of water columns determines the general availability of the resources light and nutrients for phytoplankton growth (Diehl 2002). The depth of mixing layers and/or the mixing intensity strongly affect phytoplankton primary production by influencing phytoplankton light exposure and affecting phytoplankton mortality by sedimentation (Diehl 2007; Jäger et al. 2008). However, seasonal stratification can be affected and disturbed by a-seasonal effects such as strong rain and wind events. Hence, disturbances of water column stratification imply disturbances for phytoplankton dynamics since it causes alterations in the relative supply of light and nutrients (Flöder & Sommer 1999). According to ecological theory, the frequency of disturbance strongly affects the diversity of biological communities. Whether disturbances increase or decrease the diversity of a community also depends on the productivity and the resource supply rate (Huston 1994). In environments with low nutrient supply, the same disturbance may have opposing effects on phytoplankton communities as compared to environments with high nutrient supply. This important interaction between disturbances and nutrient supply rate is, however, seldom considered in investigations of disturbance effects on plankton communities. Environmental effects on phytoplankton diversity can have extensive consequences beyond changes in species composition. Ptacnik et al. (2008) showed that diversity is the best predictor for the resource use efficiency (and thereby carbon production) and the stability of the resource use efficiency in phytoplankton communities. Consequences of these findings are that in less diverse communities resources may be more easily monopolized by bloom forming species and that phytoplankton – zooplankton interactions are less stable, possibly hampering trophic transfer (Ptacnik et al. 2008). Striebel et al. (2009a, 2009b) demonstrated that the efficiency of using the resource light, the carbon production, and the biomass composition (carbon to nutrient ratio) of freshwater phytoplankton communities is indeed related to diversity. The carbon to nutrient ratio of phytoplankton in turn is an important parameter determining nutrient recycling, transfer efficiency between phytoplankton and zooplankton, stability of phytoplankton - zooplankton interactions, and diversity of zooplankton communities (Urabe & Sterner...
1996; Sterner et al. 1997). Therefore, disturbance mediated effects of diversity on resource use and biomass stoichiometry of phytoplankton communities can have major impacts on the functioning of the entire pelagic ecosystem. Our experiments will show how species diversity, resource use efficiency and carbon production are linked within a marine phytoplankton community. We will study the relationship between water column stratification, rate of disturbance and phytoplankton diversity in marine environments. Additionally, we will investigate the link between stratification disturbance and phytoplankton diversity and its consequences for zooplankton growth in a marine pelagic community. Ciliates have population growth rates equaling or exceeding those of phytoplankton. As a result, the response to disturbance of phytoplankton in ciliate-edible size classes may be masked by changes in abundance and diversity of their ciliate grazers.

2. METHODS

We studied the responses of a natural coastal phytoplankton community to manipulations of the stratified water column. We installed 24 enclosures (10m depth) and disturbed the stratification of the water column by artificially mixing at different time intervals (1-16 days). Undisturbed mesocosms acted as controls. We established two nutrient levels, unenriched treatments and enriched treatments with a moderate supply level (0.5 µg P l\(^{-1}\) d\(^{-1}\); Si:N:P 16:16:1) compared to the natural loading of the system (Vadstein et al. 2004). We followed the response of phytoplankton, ciliates, and zooplankton communities to stratification disturbances for about 4 weeks.

Phytoplankton species composition, phytoplankton biomass stoichiometry (carbon, nitrogen and phosphorus; for each analysis filtration with GF-F filters) and dissolved nutrients were analyzed at the start of the experiment and afterwards every third day. Phytoplankton diversity will be determined from samples fixed with Lugol’s iodine with an inverted microscope using Utermöhl chambers. Phytoplankton biovolume was determined during the experiment using a cell counter (Casy® Counter). Primary productivity of the different phytoplankton communities, phytoplankton growth and loss rates (mainly grazing by micro- and mesozooplankton), were determined using the dialysis method (Stibor et al. 2006). Resource use efficiency was determined after Ptacnik et al. (2008). Detailed pigment analyses (HPLC) will be performed to investigate whether taxonomic diversity is coupled with pigment diversity (functional diversity). Ciliate samples (filtered through 100 µm mesh to exclude zooplankton), and zooplankton samples were taken (at the start of the experiment and in the following every third day) to determine abundance, species composition, and zooplankton biomass composition.

3. RESULTS

After 20 days of experimental duration, the attenuation coefficient (k) increased with increasing chlorophyll-\(a\) concentrations (Fig. 1A) while the attenuation coefficient increased only slightly with increasing disturbance frequency (Fig. 1B). We determined differences in phytoplankton biomass and in particulate nutrient concentrations between unenriched and enriched treatments (Fig. 2A-C). No differences in seston stoichiometry were seen between enriched and unenriched treatments, pointing at high turnover counterbalancing phytoplankton nutrient limitation in the unenriched mesocosms (Fig. 2 D and E). However, we found a considerable difference in chlorophyll-\(a\) levels and resource use efficiency (RUE\(_{Chl\ a}\) =ln(chl \(a\):TP)) between enriched and unenriched treatments (Fig. 2F). Moreover, RUE\(_{Chl\ a}\) exhibited a unimodal pattern with disturbance frequency in the enriched treatments. We performed dialysis experiments to determine phytoplankton growth rates and grazing losses. Growth rates (without grazing losses; share of unfiltered water = 0) were higher at 1m water depth compared to 8m water depth in both enclosures as displayed in Fig. 3. Microzooplankton grazing was high, which can be concluded by comparing the growth rates within the dialysis bags with the growth rates in the enclosures (share unfiltered water = 1; black symbols). The U-shaped curve indicates a trophic cascade within the microbial community; the minimum growth at intermediate dilution levels may reflect that grazing control of nanoflagellates by microzooplankton was alleviated here, resulting in stronger control of small-sized phytoplankton in these treatments.
Figure 1: Attenuation coefficient vs. chlorophyll-α (A) and vs. the disturbance frequency (B) treatments after 20 days of experimental duration. Black dots display unenriched treatments and white dots the enriched.

Figure 2: Phytoplankton biomass parameters related to the disturbance frequency after 20 days of experimental duration: Phytoplankton carbon (A), nitrogen (B), and phosphorus (C) content. Molar carbon to nitrogen (D) and carbon to phosphorus (E) ratios and chlorophyll-α based resource use efficiency (RUE$_{\text{Chl}}$) (F) of phytoplankton. Black dots display unenriched treatments and white dots the enriched treatments.

Figure 3: Growth rates from two daily mixed and enriched enclosures after 20 days of experimental duration at different water depths. Circles and black lines: 1m; Triangles and long dashed lines: 3m; Squares and short dashed lines: 8m water depth. Black filled symbols indicate the control samples in the enclosures (large zooplankton grazing possible).
4. CONCLUSIONS

We proposed to analyze the above described un-investigated links between disturbances of water column stratification and diversity and its consequences for marine plankton dynamics in a gradient of disturbances at different nutrient supply rates in a large scale mesocosm experiment. We analyzed the relationships between disturbance of water column stratification and phytoplankton diversity, diversity dependent resource use efficiency, the stability of resource use efficiency (and carbon production), and between diversity dependent carbon dynamics of phytoplankton communities and zooplankton growth. As we are currently analyzing our results and counting phytoplankton, ciliate, and zooplankton samples, the data shown here are only preliminary results. With our experiments we will show how phytoplankton diversity, productivity and resource use efficiency are linked within a marine community and how stratification disturbance will influence this community. Furthermore, our results will show the impact of these disturbance induced changes in the phytoplankton community on ciliate and on zooplankton dynamics (growth and diversity).

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