



Stability of marine phytoplankton communities facing stress related to global change: Interactive effects of heat waves and turbidity



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ABSTRACT

According to climate models, coastal ecosystems will face an increased frequency of heat waves and increased turbidity due to terrestrial sediment run-off induced by increasing precipitation. Several studies have examined the effects of heat waves and turbidity separately, whereas this study analysed the individual effects of both stressors as well as their interaction, because stressors affect communities differently when acting in combination. Using a factorial experimental design, we simulated heat waves (22 °C and 26 °C compared to an 18 °C control) and turbidity (sediment addition). The response of the phytoplankton community was analysed for the aggregate parameters biovolume and diversity index (H'), as well as for community composition. Heat waves had a significant negative effect on biovolume, whereas turbidity tended to affect biovolume positively. Repeated measures ANOVA revealed significant interactions of heat waves and turbidity for H' and community composition. Strong heat waves (26 °C) alleviated the otherwise positive effect of turbidity on H' , i.e. highest diversity remained in the turbid control. Diatoms gained dominance in the control and the 22 °C heat wave treatment with *Cylindrotheca closterium* being the successful competitor. At 26 °C this species was lost and small flagellates dominated the experimental communities. Future increases in heat wave intensity and frequency may thus induce major changes in phytoplankton community structure whereas algae might profit from increased turbidity as an additional source of nutrients.

1. Introduction

Global environmental change, in particular warming, influences ecosystem composition in aquatic and terrestrial systems (Burgmer et al., 2007; Seifert et al., 2015; Stocker, 2014; Stocker et al., 2014). Elevated sea surface temperature causes rapid changes in aquatic communities including changes in the abundance and spatial or seasonal distribution of marine phytoplankton as well as temporal mismatches between trophic levels (Field et al., 2014; Poloczanska et al., 2013; Thiede et al., 2016). There is an ongoing debate whether altered stratification and species composition will lead to a global decline in phytoplankton productivity (Boyce et al., 2010; Lewandowska et al., 2012; McQuatters-Gollop et al., 2011), which would be a severe change of the Earth system as marine phytoplankton provides nearly half of the global primary production (Behrenfeld et al., 2006; Thomas et al., 2012; Valiela, 2013). Additionally, phytoplankton in the ocean plays a major role in the global carbon, nitrogen and phosphorous cycles (Thomas et al., 2012) and as a base of marine food webs. A change in phytoplankton biodiversity and abundance will thus ultimately have

consequences for higher organisms as well as for the economy with regard to fisheries (Hays et al., 2005).

Depending on the emission scenario of the intergovernmental panel on climate change (IPCC), future temperature will rise between 2 °C and 5 °C by the end of the 21st century (Field et al., 2014). The ocean stores 90% of the planet's heat content and since the 1970s, water temperature, particularly close to the surface, has warmed already 0.11 °C per decade (Boyd et al., 2010; Field et al., 2014). This process is likely to continue and especially latitudes > 40° are warming increasingly (Poloczanska et al., 2013). On a regional scale, sea surface temperatures in the North Sea have risen more than in any other area of the North-East Atlantic over the past 25 years, with temperature increases of 1 °C to 2 °C and a further predicted increase of 2.5 °C (Steege and Köthe, 2015; Thiede et al., 2016).

Most studies evaluate the consequences of such changes in mean annual temperature, but also the frequency and intensity of heat waves is likely to increase (Field et al., 2014; Hov et al., 2013). Heat waves, in this context, are defined as a period of at least three to five days during which mean or maximum temperature anomalies were at least 3–5 °C

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above normal (Hobday et al., 2016; Meehl and Tebaldi, 2004). Such heat waves affect marine ecosystems with respect to invertebrate, fish and macroalgal mortality, and the occurrence of algal blooms, as events in the North-western Mediterranean in 2003 (Garrabou et al., 2009) and heat waves in 2011 along the western Australian coast (Moore et al., 2012; Rose et al., 2012) have shown.

In addition to other effects of global change, like ocean acidification and sea level rise, increasing windiness and rainfall reduced light availability in the North Sea over the second half of the 20th century (Capuzzo et al., 2015). Further sources for additional sediment input into the ocean are coastal erosion and rivers. Although increasing coastal erosion is related to changes in wind and wave activity (Capuzzo et al., 2015), evidence for increased sediment fluxes from rivers to oceans varies strongly between world regions depending for instance on precipitation and the existence of dams and water reservoirs (Walling, 2009). Yet, the predicted increase in precipitation will likely affect sediment run-off and resuspension.

This study analyses the effects caused by heat waves and turbidity on phytoplankton communities. Particular focus lies on the interaction of the two stressors because in natural systems stressors usually act in combination (Flöder and Hillebrand, 2012; Folt et al., 1999; Segner et al., 2014). Individual physiological processes as well as ecological interactions are interdependent, which makes an interaction of stressors very likely (Breitburg and Riedel, 2005). However, it is more difficult to examine the effects of multiple stressors than of single stressors and it is unfeasible to assess all combinations of multiple stressors (Hooper et al., 2013). Therefore, stressors are often tested individually in laboratory experiments. The focus is thereby on the properties of the stressor instead of the traits of the biological receptor, for instance marine phytoplankton, which would ultimately show a species-specific reaction toward the stressor (Segner et al., 2014). This sometimes leads to surprising results when combined stressors are examined, because the effects can be less, larger or qualitatively different than what was predicted from individual stressors (Breitburg and Riedel, 2005; Segner et al., 2014).

Although the response of phytoplankton to temperature and turbidity as single stressors has been well studied (Behrenfeld et al., 2006; Boyce et al., 2010; de Jorge and van Beusekom, 1995; Dzialowski et al., 2008; Lewandowska et al., 2012; Seifert et al., 2015; Sloth et al., 1996), until recently, only few studies have analysed the effect of temperature in combination with turbidity (Zehrer et al., 2015). As temperature has direct metabolic effects on cellular processes and often interacts with other factors such as light and nutrients (Boyd et al., 2010), this study focuses on the effects of an interaction between heat wave and turbidity on biovolume, diversity (number of species and their relative abundance as defined by the diversity index H' (see Washington, 1984) and taxonomic composition of an assembled phytoplankton community. We used a factorial approach to examine the effects of multiple stressors, temperature and turbidity, on the stability of a phytoplankton community and to answer the following research questions:

- 1) What effects do the stressors heat wave and turbidity have on the phytoplankton community, when they are applied separately?
- 2) When applied simultaneously, what kind of interaction will there be between heat wave and turbidity?
- 3) How severely is the stability of the phytoplankton community affected and to what degree does it recover?

2. Materials and methods

2.1. Experimental conditions

Four phytoplankton groups were used for the study: diatoms (*Coscinodiscus granii*, *Leptocylindrus danicus*, *Thalassiosira* sp., *Pseudonitzschia* sp., *Cylindrotheca closterium*, *Chaetoceros* sp.), chlorophyceae (*Chlamydomonas* sp.), dinoflagellates (*Prorocentrum micans*,

Scrippsiella trochoideae) and cryptophyceae (*Rhodomonas salina*). These microalgae belong to principle taxa of phytoplankton and are cosmopolitan and species that also occur in the North Sea (Boyd et al., 2010).

The algae were taken from the ICBM culture collection and grown on f/2-Medium (Guillard, 1975; Guillard and Ryther, 1962). During the experiment, phytoplankton communities (150 mL in Erlenmeyer flasks) were grown semi-continuously whereby 50 mL of medium was exchanged three times a week under sterile conditions. The experiment was conducted in a constant temperature room (18 °C). Light intensity was 40–45 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, with a day-night-cycle of 12 h. The algae were kept in suspension using a shaker-table (100 rpm). To compensate for the slightly uneven lighting, the experimental cultures were randomly arranged on the shaker-table and their position was changed, whenever culturing work was done.

2.2. Experimental design

As we aimed to examine the effects of two combined stressors, heat wave and turbidity, three different temperature levels (18 °C, 22 °C, 26 °C) were established and half of the respective replicates were additionally treated with sediment to simulate turbidity. Temperature levels were chosen with regard to a possible temperature development during heat waves in temperate waters, like the North Sea, as well as with regard to marine heat waves that have already occurred (Garrabou et al., 2009). The control was kept at 18 °C, simulating warm summer temperature in the North Sea (Loewe et al., 2013). Heat waves lasted for 14 days and peaked at 26 °C for the extreme heat wave (+ 8 °C) and 22 °C (+ 4 °C) for the moderate heat wave, respectively. The increases in temperature were achieved with a heating pad (Biogreen “Heating-mat Sahara”) underlying the Erlenmeyer flasks. A layer of fine grained sand ensured an equal heat distribution.

For the turbidity treatment, natural sediment was used. It was collected from the surface (upper 1–2 cm) of the Jade Bight on 22.09.2015. After drying the sediment at 65 °C and heat sterilization (170 °C for 2 h), the sediment was homogenised using a ball mill and subsequently fractionated with a set of analytical sieves. Only the sediment fraction with a particle size < 160 μm was used and 0.6 g L⁻¹ was added to each replicate of the turbidity treatment.

The experimental set-up consisted of 24 Erlenmeyer flasks. Always eight flasks represented one temperature treatment of which four flasks were additionally treated with sediment (2 × 4 × 3 = 24 experimental units). The experiment was run for four weeks from 02.11.2015 to 30.11.2015.

Before starting the experiment, 20 cells of each phytoplankton species were measured with the computer program “CellP” (Olympus Soft Imaging Solutions GmbH). Average individual biovolume was calculated according to Hillebrand et al. (1999) and Olenina et al. (2006). The experimental units were inoculated with all species contributing the same biovolume (216.6 10⁻⁶ mm³ mL⁻¹). The nutrient concentrations of the f/2-medium (432 $\mu\text{mol N L}^{-1}$, 13.5 $\mu\text{mol P L}^{-1}$, 98 $\mu\text{mol Si L}^{-1}$) were higher than those that naturally occur in the North Sea (for 2000–2007: 45–50 $\mu\text{mol N L}^{-1}$, 0.9–1.1 $\mu\text{mol P L}^{-1}$, 25–30 $\mu\text{mol Si L}^{-1}$ (Loewe et al., 2013). Through nutrient saturation we wanted to make sure that a potential turbidity effect did not derive from additional nutrient supply. Although all nutrients were provided in great quantity, the effect was not derived.

The algae were grown for five days before the stressor regime began. On day five, sediment was added and the temperature treatment was started. The temperature was intended to remain stable for the following 14 days, whereas due to the semi-continuous design turbidity would decrease over time. From high turbidity after addition, the sediment would be washed out toward the end of the experiment (Fig. 1). Water temperature was monitored daily with an analogue thermometer and from day eleven on with a HOBO data logger in a separate Erlenmeyer flask for each higher temperature treatment. From day 5, temperature was relatively stable for the 22 °C treatment (21.9 °C ± 0.4 °C

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