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Physiological constraints on the global distribution of *Trichodesmium* – effect of temperature on diazotrophy

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Abstract

The cyanobacterium *Trichodesmium* is an important link in the global nitrogen cycle due to its significant input of atmospheric nitrogen into the ocean. Incorporating *Trichodesmium* in ocean biogeochemical circulation models relies on field-based correlations between temperature and *Trichodesmium* abundance. The observed correlation of *Trichodesmium* abundance with temperature in the ocean may result in part from a direct effect on *Trichodesmium* growth rates through the control of cellular biochemical processes, or indirectly through its influence on mixed layer depth, light and nutrient regimes. Here we present results indicating that the observed correlation of *Trichodesmium* with temperature in the field reflects primarily the direct physiological effects of temperature on diazotrophic growth of *Trichodesmium. Trichodesmium* IMS-101 (an isolate of *T. erythraeum*) could acclimate and grow at temperatures ranging from 20 to 34°C. Maximum growth rates (μ_{max}=0.25 day^{-1}) and maximum nitrogen fixation rates (0.13 mmol N mol POC^{-1} h^{-1}) were measured within 24 to 30°C. This empirical relationship and global warming scenarios derived from state-of-the-art climate models set a physiological constraint on the future distribution of *Trichodesmium* that could significantly affect nitrogen input into oligotrophic waters by this diazotroph.

1 Introduction

The diazotrophic filamentous cyanobacterium *Trichodesmium* plays a central role in the nitrogen and carbon cycle of oligotrophic oceans, contributing up to 80 Tg of fixed nitrogen yr^{-1} (Capone et al., 1997). This represents a major fraction of the total marine nitrogen fixation, currently estimated at 110 Tg yr^{-1}(Gruber and Sarmiento, 1997). Furthermore, *Trichodesmium* can account for up to 47% of the primary production in the tropical North Atlantic Ocean (Carpenter et al., 2004) and contributes to export production via nitrogen fueling of the phytoplankton community (Letelier and Karl, 1996; Karl et al., 1997). *Trichodesmium* abundance is generally limited to oligotrophic wa-

ters and its observed temperature distribution range (20°C–30°C) is used to constrain N_2-fixation in ocean biogeochemical circulation models (OCBM) (Fennel et al., 2001; Hood et al., 2001, 2004). The upper temperature limit is set by current sea surface temperature (SST) maxima and not by observed physiological constraints of high temperature on *Trichodesmium* distribution. Parameterizations are based solely on field correlations and cannot differentiate between direct and indirect effects of temperature on *Trichodesmium* growth and thus are of limited predictive value.

Distribution to higher latitudes with water temperatures below 20°C appears to be due to drift rather then net growth. Nitrogen fixation by *Trichodesmium* was not observed in theses waters (Carpenter, 1983; Lipschultz and Owens, 1996), whereas diazotrophic growth at temperatures close to freezing by other cyanobacteria, i.e. *Oscillatoria* sp. (Pandey et al., 2004) or *Nostoc* sp. (Zielke et al., 2002), is possible. An upper temperature limit cannot readily be derived from field observations because the present sea surface temperatures rarely reach the observed upper tolerance limit for *Trichodesmium* in tropical waters (Capone et al., 1997). A few exceptions are found where blooms of *Trichodesmium* have been reported at water temperatures as high as 35°C, however, these high temperatures may have been due to surface heating by heat absorption of the dense *Trichodesmium* mat and probably resulted in rapid cell lysis and death (Capone et al., 1998).

While empirical field correlations may be useful for parameterization of models, they provide no information on the direct physiological effect of temperature on the growth, nitrogen fixation and C:N stoichiometry in *Trichodesmium*. A parameterization of models using a physiological basis for the apparent temperature control of *Trichodesmium* distribution would provide an additional predictive value. Here we present the effect of temperature on nitrogen fixation, POC:PON and Chl-*a*:POC stoichiometry, and growth for *Trichodesmium* IMS-101. We discuss the possible physiological basis for this relationship relative to other factors, such as light and nutrients, also affecting the distribution of *Trichodesmium*. Based on climate change scenarios and their effect on sea surface temperature increase within this century, we point out the importance of un-

derstanding the physiology of *Trichodesmium* for their incorporation in OBCM and for predicting oceanic nitrogen input by this diazotroph in the future.

2 Materials and methods

2.1 Growth of cultures

An axenic culture of *Trichodesmium* IMS-101 was grown at temperatures ranging between 15 and 36°C for at least three transfers (minimum of 15 generations) at each temperature, under a light:dark cycle of 12:12 h and a light intensity of 100 μmol quanta $m^{-2}s^{-1}$ using phosphorus and iron replete YBC II media without dissolved nitrogen added (Chen et al., 1996). Three independent attempts were made to acclimate *Trichodesmium* to grow at temperatures lower than 20°C and above 34°C. The cultures were transferred from the respective higher or lower temperatures where growth was detected as well as from well-growing cultures incubated at 25°C.

2.2 Nitrogen fixation measurements

Nitrogen fixation rates were measured using the Acetylene Reduction Assay (ARA) (Capone, 1993), while calculations were modified after Breitbarth et al. (2004) and a ratio of C_2H_2 reduced: N_2 reduced of 4:1 was used (Montoya et al., 1996). Gas samples were analyzed on a Shimadzu GC-19B equipped with a flame ionization detector and a 30 m wide bore capillary column (0.53 mm, AluminaPlot®, Resteck, USA). The oven temperature was set at 40°C, injector and detector temperature at 200°C, and the carrier gas flow (N_2) at 14.5 ml min^{-1}, which yielded optimal peak separation and detection limits. Three replicates for each temperature were incubated simultaneously for 4 h in 20.2 ml headspace vials containing 19 ml culture and 1.2 ml headspace with 0.4 ml acetylene added. ARAs were carried out for three individual times on semi-continuously growing cultures. Nitrogen fixation rates were normalized to POC.

2.3 Biomass and elemental stoichiometry

For biomass determinations, samples were filtered (GF/F, pre-combusted for elemental analysis) and stored at −20°C until further analysis. Particulate organic nitrogen (PON) and particulate organic carbon (POC) contents of the cultures were determined after Sharp (1975) and Ehrhard and Koeve (1999). Frozen filters were dried for 48 h at 45°C and thereafter measured using an elemental analyzer (Euro-EA, Hekatech, Germany) equipped with a chromium-oxid/cobalt-oxid oxidation reactor, a copper reduction reactor, and a CHN column at an oven temperature of 45°C. Carrier gas flow (He) was set at 96 ml min^{-1}. The data were blank corrected using measurements of similarly treated filters without culture material.

The chlorophyll-*a* concentrations were analyzed fluorometrically based on Welschmeyer (1994) after bursting the cells in 90% Acetone by shaking and refreezing for 24 h. Results obtained from this simple extraction method were comparable to those made by mechanical disruption of the cells (data not shown).

Maximum specific growth rates (μ) were determined by identifying the exponential growth phase in the batch cultures and applying a linear fit to the respective natural logarithm transformed POC, PON and Chl-*a* values. The slope of the regression represents the growth rate.

2.4 Photosystem response measurements

The photosynthetic quantum use efficiency of the photosystem II was measured using a PhytoPAM equipped with Optical Unit ED-101US/MP (Walz, Germany) based on Kolbowski and Schreiber (1995). The ratios of variable to maximal fluorescence (F_v/F_m) of *Trichodesmium* IMS-101 in response to different incubation temperatures were recorded over the complete growth period of the cultures at the respective temperatures. Further, F_v/F_m was measured on cultures grown at 25°C after short-term exposure (4 h) to a temperature range of 14°C to 36°C. Samples were dark-adapted for 10 min prior to the measurements.

2.5 Sea surface temperature increase predictions

Predictions of the increase in sea surface temperature (SST) were based on two coupled atmosphere-ocean general circulation models (HadCM3 and GFDL) to current annual SST (Levitus and Boyer, 1994). Both models predict a SST increase of up to 3°C by 2090 in our area of interest (20–30°C isotherms). The HadCM3 model run (Gordon et al., 2000) is based on the assumption that future emissions of greenhouse gases will follow the IS92a "business as usual" scenario with observed atmospheric CO_2 concentrations until 1990 and a 1% annual increase thereafter (http://www.met-office.gov.uk/research/hadleycentre/models/modeldata.html).

This prognosis is generally consistent with results from a similar experiment using the GFDL R30 climate model (Delworth et al., 2002) (http://www.gfdl.noaa.gov/~kd/ClimateDynamics/NOMADS/index.html). The SST changes predicted by the climate models over the next century are then added to current mean SSTs and the area of various physiologically relevant temperature ranges is computed.

3 Results

3.1 Growth and nitrogen fixation

Our results demonstrate that *Trichodesmium* IMS-101 grows and fixes nitrogen at temperatures between 20–34°C (Fig. 1). The cultures did not grow below 20°C or above 34°C. Cultures could be maintained alive at 17°C for several weeks, but biomass progressively decreased. Incubations at water temperatures of 36°C resulted in cell death and lysis after two days (data not shown). Growth rates did not differ significantly between chlorophyll–*a*, carbon or nitrogen specific growth, with the exception of carbon and nitrogen specific growth rates being higher than chlorophyll specific growth rates at 30°C. No differences in growth rates were detected, when cultures were transferred from similar or adjacent incubation temperatures or originated from 25°C incu-

bations. Maximum specific growth rates (μ_{max}) of the axenic *Trichodesmium* IMS-101 strain were optimum between 24–30°C, with a peak at 27°C (μ_{max} carbon specific=0.25 day^{-1}, Fig. 1). Growth rates were significantly reduced below and above this temperature range.

Nitrogen fixation rates were significantly affected by temperature and followed closely the relationship observed for growth rate versus temperature, showing a temperature optimum between 24–30°C as well. Maximum nitrogen fixation rates of 0.13 mmol N mol POC^{-1} h^{-1} were measured at 27°C. Triplicate experiments with semi-continuously growing cultures yielded similar temperature relationships (Fig. 1).

3.2 Elemental stoichiometry

These observations were supported by measurements of elemental stoichiometry. The cellular carbon to nitrogen ratio increased from 5.4 (mol:mol) at 20°C to a maximum of 6.8 at 25°C. This ratio equals approximately the Redfield ratio (6.6). At higher temperatures the POC:PON stoichiometry decreased again to a minimum value of 4.1 at 34°C (Fig. 2). The data shown are derived from measurements throughout the growth period of the batch incubations. As previously reported by Mulholland and Capone (2001), POC:PON ratios varied over the growth period and were reduced during the exponential growth phase, which is a characteristic of high N_2-fixation. A comparatively high POC:PON stoichiometry was measured at 17°C (9.1). However, it is not clear whether or not this is an artifact created because *Trichodesmium* could not grow at this low temperature.

Further, the cellular chlorophyll-a to carbon ratio increased linearly from 0.0044 (g:g) at 17°C to 0.0194 at 34°C (Fig. 3a) reflecting an acclimation response of the photosynthetic apparatus to temperature (Geider et al., 1997).

3.3 Photosystem response

The photosynthetic quantum yield efficiency (F_v/F_m) of cultures acclimated to their growth temperature increased from below 0.10 at 17°C up to a maximum quantum yield of 0.68 at 30°C. As there was considerable variation of Fv/Fm as a function of physiological differences during growth in batch cultures, only samples from the exponential growth phase were plotted in Fig. 4a. Here, the average quantum yield efficiency increased from 0.20 at the minimum feasible growth temperature (20°C) to 0.52 at 27°C and remained constant up to 34°C. Maximum values did not exceed 0.60 (Fig. 4a). In contrast, F_v/F_m measurements of *Trichodesmium* grown at 25°C and transferred to a range of temperatures (4 h incubations) were positively correlated with temperature and increased linearly from approximately 0.25 at 14°C to the maximum of 0.60 at the maximum growth temperature (34°C). This demonstrates that the photosynthetic apparatus adjusted slowly to changes in temperature. Measurements at 36°C showed reduced F_v/F_m values again (Fig. 4b).

3.4 Potential effects of predicted SST increase on Trichodesmium distribution

The modeled sea surface temperature (SST) increase of up to 3°C by 2090 in our area of interest (20–30°C isotherms) predicts a poleward shift of the 20°C isotherm (Fig. 5). This results in an 11% areal increase of *Trichodesmium's* potential geographic distribution. Second, maximum calculated SSTs will still be less than 34°C, which will not limit the potential distribution of *Trichodesmium* in tropical waters. Nevertheless, a decrease in the area characterized by optimum growth and N_2-fixation conditions (24–30°C) by about 16% is anticipated (Fig. 5).

4 Discussion

Temperature per se does not restrict diazotrophic growth and nitrogen fixers can be encountered at temperatures close to freezing (Zielke et al., 2002; Pandey et al., 2004),

yet the overall distribution of *Trichodesmium* in the contemporary ocean appears well constrained by seawater temperature (~20–30°C)(Capone et al., 1997). However, the correlation of water temperature with *Trichodesmium* abundance is generally attributed to oceanographic features associated with warm waters, such as shallow mixed layer depth, high light regimes and oligotrophic nutrient conditions rather than a direct physiological response to temperature itself (Hood et al., 2004). Since water temperature and dissolved nitrate concentrations are significantly negatively correlated in the marine environment, it is not certain whether the global patterns of N_2-fixation versus water temperature are due to an inhibition of nitrogenase by low temperature or a selection against N_2-fixers under conditions of high nitrate or both. In this work, we separated the effect of temperature from other factors (i.e. nutrients, light, and stratification) on diazotrophic growth and thus were able to demonstrate that, as suggested by Capone et al. (1997), seawater temperature sets a physiological constraint on the geographic distribution of *Trichodesmium.*

We were able to demonstrate that the strain IMS-101 of *Trichodesmium* is adapted to optimum growth temperatures between 24 and 30°C, and can tolerate water temperatures from 20 to 34°C. Analogous to our results, positive correlations of *Trichodesmium* abundance and water temperature (22–28/31°C) were also observed in field studies (Capone et al., 1997; Lin, 2002; Lugomela et al., 2002; Chen et al., 2003). However, our observation that cells can survive at 17°C for several weeks and experience a slow decrease in biomass, can also explain the persistence of *Trichodesmium* transported into higher latitudes by oceanic currents (Carpenter, 1983; Lipschultz and Owens, 1996).

In contrast to our finding of an optimum temperature rage between 24 and 30°C, Staal et al. (2003) described a linear increase of nitrogen fixation up to a temperature of 36°C in short-term incubations (2 min, M. Staal, personal communication). Measurements published by Staal et al. (2003) most likely reflected nitrogenase enzyme kinetics, whereas data presented here describe temperature acclimated diazotrophic growth (Fig. 1). This is based on the physiologic patterns of maximum nitrogen fixa-

tion activity, highest growth rates, cellular elemental composition, and photosynthetic quantum yield efficiency. The maximum growth rates and high nitrogen fixation rates between 24 and 30°C must be accompanied by high carbon fixation rates, which is expressed in near Redfield POC:PON stoichiometry. At lower or higher temperatures the POC:PON ratio was reduced. This stoichiometric shift can be due to high nitrogen to carbon incorporation rates and may reflect the relative distribution of photochemical energy utilization between carbon fixation and nitrogen fixation. At the low end of the temperature tolerance range, both carbon fixation and nitrogen fixation may be energy limited, driving the POC:PON ratio close to that of pure protein (Geider and La Roche, 2002), while the reduced POC:PON ratio at higher temperatures may reflect increased carbon respiration rates (Fig. 3). As an effect of temperature though, a larger fraction of fixed N_2 may be released and not incorporated into the cells when either carbon fixation is insufficient, or cells may become leakier due to increased membrane permeability at higher temperatures. The temperature acclimation of the chlorophyll-a:POC ratio reflects the need to reduce light absorption at low temperatures in order to equilibrate with lower enzyme activity, while this mechanism is relieved at higher temperatures. Factors, such as light and nutrient regimes directly interact with temperature and will also play determinant roles. Photosynthetic organisms will acclimate to both light and temperature, by adjusting the balance between light energy absorption and the rate of the dark reaction of photosynthesis, however in an opposite way, i.e. by increasing light absorption in low light and decreasing it at low temperature (Geider et al., 1997; Miskiewicz et al., 2002). The photosynthetic quantum use efficiency clearly reflects a physiological adaptation to the temperature tolerance range of *Trichodesmium* (IMS-101). In short term incubations F_v/F_m measurements increased linear up to the physiological maximum temperature of 34°C. Measurements of cultures growing exponentially at the respective temperatures though reveal that the photosystem II operated at minimum efficiency at 20°C and saturated at maximum efficiencies between 27 and 34°C. Thus, the temperature tolerance range of *Trichodesmium* IMS-101 grown at 100 μmol quanta $m^{-2}s^{-1}$ is also confined by the general range of photosynthetic quan-

tum yield efficiency for cyanobacteria (0.20–0.60, Fig. 4a). One can hypothesize that the high temperature optimum for *Trichodesmium* growth leads to a better tolerance of high light intensity, which is characteristic of tropical and sub-tropical regions.

While we cannot fully explain the biochemical basis for the physiological constraint to the observed temperature range, a combination of several mechanisms is likely. In *Trichodesmium*, the timing of nitrogen fixation and photosynthesis has been shown to be under the control of a circadian rhythm (Chen et al., 1998) and the temperature tolerance range may be in part set by the temperature compensation range of the circadian clock. Further, the photochemical reactions themselves are temperature dependent due to enzyme kinetics and membrane permeability (Falkowski and Raven, 1997). It has been shown for terrestrial plants that Rubisco activase has a lower temperature tolerance than Rubisco itself. Rubisco activase is not capable of maintaining Rubisco in an active form at growth temperatures outside the thermal environment to which the organism is adapted to (Crafts-Brandner and Salvucci, 2000; Salvucci and Crafts-Brandner, 2004a, b). It is possible, but remains to be demonstrated, that such a mechanism also limits the photophysiology of *Trichodesmium* at the high end of the temperature tolerance range.

Overall, the mechanisms determining the optimal growth temperature in microorganisms are poorly characterized but, at the most basic level, must be controlled by their genetic composition. Genomic analysis of psychrophilic bacteria revealed that cold-adaptation is not just a function of a specific set of proteins but also dependent on the general amino acid composition of the proteins and membrane fluidity and permeability (Methe et al., 2005). Diazotrophs in general can grow at all temperatures. In particular, *Oscillatoria*, a close relative of *Trichodesmium* is found in the Antarctic (Pandey et al., 2004). Phylogenetic analysis of the hetR gene, which is most likely involved in heterocyst and diazocyst development, revealed a high diversity level within the *Trichodesmium* clade (Mes and Stal, 2005). Thus, although the strain *Trichodesmium* IMS-101 did not adapt to growth at higher and lower temperatures in our experiments, other uncultivated strains may be capable of growth outside this temperature range.

Acknowledging that we lack information on the physiological variability within the genus *Trichodesmium*, we carefully suggest that future changes in SST may result in an 11% areal increase of *Trichodesmium's* potential geographic distribution due to the poleward shift of the 20°C isotherm, while the maximum calculated SSTs (34°C) will not be limiting diazotrophy of *Trichodesmium* in tropical waters. However, because of the much higher N_2-fixation rates and the growth physiology of *Trichodesmium* in the 24–30°C SST range, the effect of the 16% decrease in the area characterized by optimum growth and N_2-fixation conditions (24–30°C) is likely to outweigh the positive effect of the latitudinal increase of the total area (Fig. 5). Thus, the predicted over all sea surface temperature increase may result in a net decrease of N_2-fixation by *Trichodesmium* by the end of this century. The effects on oceanic nitrogen cycling may be significant, taken the global importance of this diazotroph into account (Capone et al., 1997; Capone and Carpenter, 1999). As aforementioned, these predictions are based solely on the growth temperature relationship for *Trichodesmium* IMS-101. Additionally, our hypothesis is based on SST only and does not account for possible changes in nutrient supply and light conditions, which will also be affected by SST increase and to date, are more difficult to predict than SST.

To date, predictions of future marine nitrogen fixation diverge. In contrast to our findings, Boyd and Doney (2002) predict a future increase of N_2-fixation by 27% (from 80 to 94 $\mathrm{Tg\,yr^{-1}}$) due to a floristic shift towards diazotrophy by *Trichodesmium* caused by combined effects of mixed layer depth (MLD), stratification, and nutrient regimes. Time series measurements near Hawaii (Karl et al., 1997) support this trend. Although, SSTs in this area of the North Pacific are estimated to increase by almost 3°C (Figs. 5a+b) they do not exceed the physiologically optimal range. Nevertheless, large regions of the tropical and subtropical oceans are predicted to fall outside the optimal range. Particularly temperatures rising above 30°C in N_2-fixation hotspots may result in significant changes of the regional nitrogen budgets. In the North Atlantic, for example, SSTs are predicted to exceed 30°C in the Caribbean Sea as well as in equatorial waters off West Africa, all of which are currently hotspots of N_2 fixation in a

model based on field observations, MLD and light (Hood et al., 2004). Similarly high SSTs are predicted for the western Pacific and a large part of the Indian Ocean, which both are characteristic provinces for present-day *Trichodesmium* abundance (LaRoche and Breitbarth, 2005).

Whether or not a global SST increase in the future ocean will result in a decrease in *Trichodesmium* rests on the physiological bases for the temperature dependence of nitrogen fixation and on the relative importance of temperature with regards to other factors such as water column stability, nutrient availability and light intensity. Conversely, the development of nitrogen fixation hotspots in the future ocean largely depends on feasible physical and chemical conditions in addition to temperature.

A community shift towards other (unicellular) diazotrophs is also possible. Until recently, the significance of unicellular N_2-fixers has been underestimated (Montoya et al., 2004). Although many of the unicellular diazotrophic cyanobacteria are not yet cultured, the obtainable information, either from field evidence or from the few available isolates suggest that these groups also have temperature optima in the range of 26–30°C (Mazard et al., 2004; Falcón et al., 2005). In the tropical/sub-tropical North Atlantic Ocean *nifH* genes, indicative of the presence of diazotrophs, were recovered from water temperatures between 20 and 30°C, and were mostly prominent between 26–30°C. However, a few samples from temperatures below 20°C also contained *nifH* genes, suggesting that some marine diazotrophs may also dwell in cold water (Langlois et al., 2005). Whether or not these unicellular cyanobacteria are actively fixing nitrogen, or if they can potentially fill niches for nitrogen fixers at the lower or higher temperature range remains to be investigated.

In conclusion, our results demonstrate that the temperature adaptation of *Trichodesmium* IMS-101 controls the geographic distribution of this species. Based on the physiological constraints of diazotrophic growth of *Trichodesmium* IMS-101, we suggest reduced fixed nitrogen input by *Trichodesmium* in response to the SST increase predicted for the end of this century. Although SSTs are expected to rise essentially everywhere, the area of surface waters with temperatures in the physiologically op-

timal range for growth of *Trichodesmium* will likely decline. We expect that, within the areal limits imposed by the SST, a combination of other controlling factors such as MLD, light, and nutrient regimes (including iron) will further restrict *Trichodesmium* distribution. Considering the large fraction of N_2-fixation by *Trichodesmium* on total oceanic nitrogen input, the predicted ecophysiological changes to this diazotroph may cause significant changes in global biogeochemical cycles. Nevertheless, because little is known about temperature selection on other diazotrophs, we do not know what the overall dynamics of N_2 fixation in the future ocean will be. As N_2-fixation in currently available ocean biogeochemical circulation models is based on *Trichodesmium*, it may be necessary to adjust their parameterizations with regard to the here presented temperature-diazotrophic growth relationships in addition of taking other diazotrophs into account.

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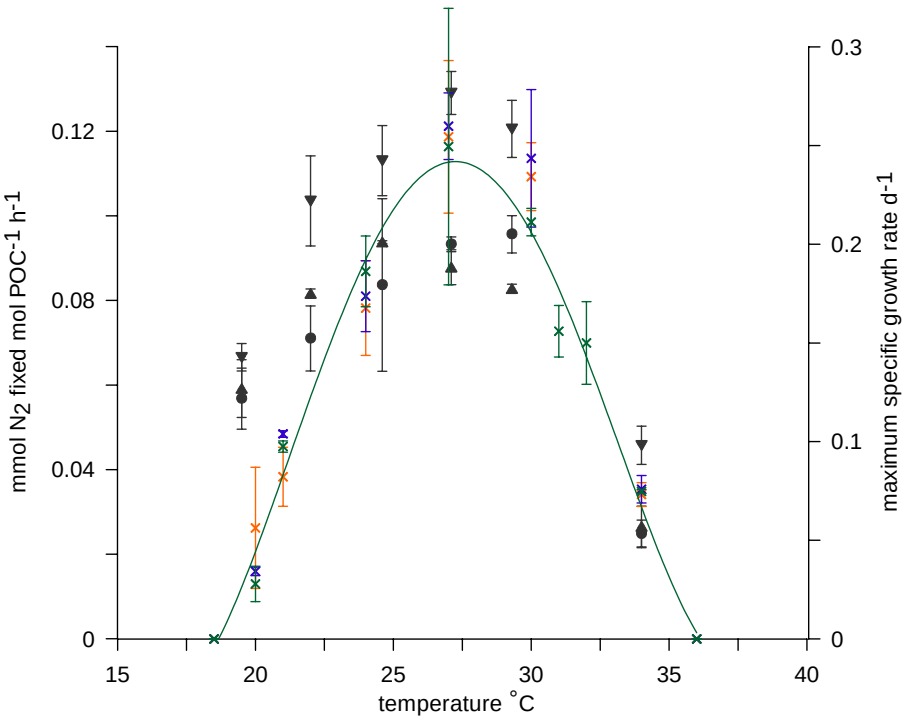

Fig. 1. Maximum carbon (x, orange), nitrogen (x, blue) and chlorophyll–*a* (x, green) specific growth rates as a function of temperature. The green line denotes the function of chlorophyll-a specific growth based on the polynomial function:

$$\mu = 2.29^{-5}x^4 - 2.50^{-3}x^3 + 9.71^{-2}x^2 + 1.58x + 9.15 \quad (1)$$

where x denotes temperature in °C. Black triangles and circles describe carbon specific nitrogen fixation rates as a function of temperature. Different symbols denote individual measurement series.

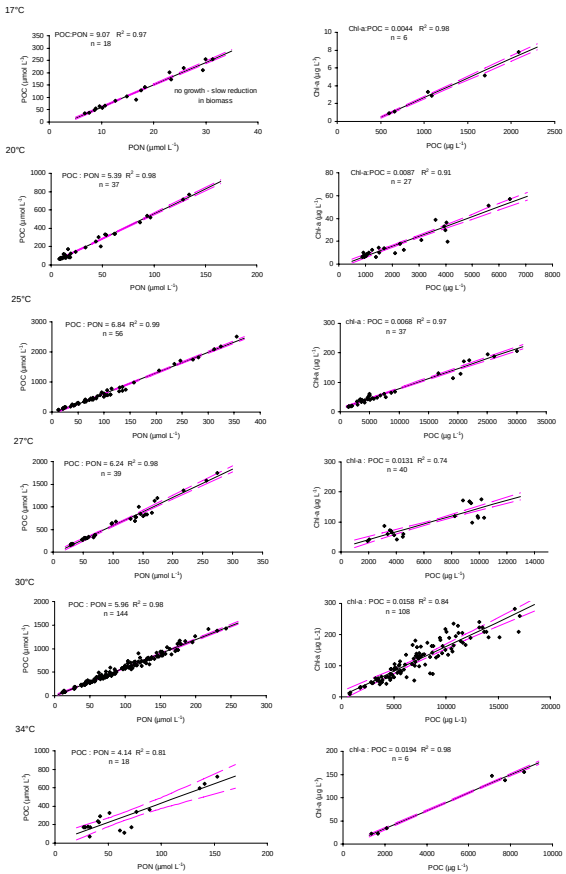

Fig. 2. Overview of POC:PON (mol:mol) and chl-a:POC (weight:weight) stoichiometry of *Trichodesmium* IMS-101 versus temperature. Solid lines describe regressions of the data versus temperature. The regression coefficient represents the stoichiometric ratio and is included in each plot together with the coefficient of determination (R^2) and the sample size (n).

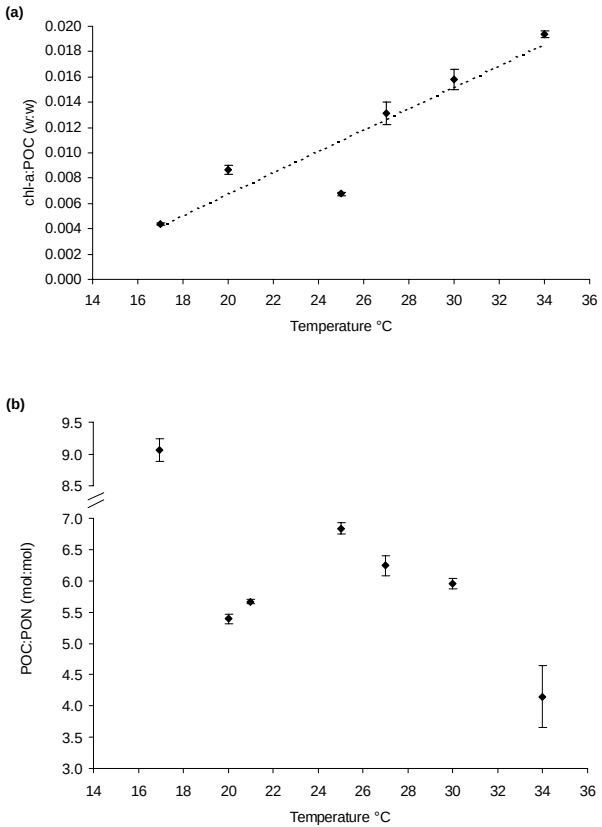

Fig. 3. Stoichiometry chl-a:POC (weight:weight, **(a)** and POC:PON (mol:mol, **(b)** of *Trichodesmium* IMS-101 as a function of growth temperature. Data points represent regression coefficients of the stoichiometric ratios at the respective temperatures and error bars denote the standard error of the regression coefficients. The dotted line represents a linear fit to the data points.

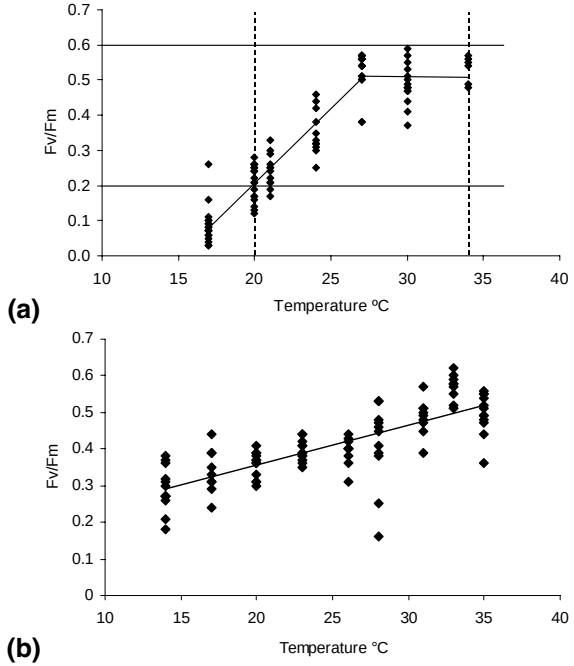

Fig. 4. (a): Photosynthetic quantum use efficiency of only exponentially growing *Trichodesmium* IMS-101 batch cultures acclimated to the respective temperatures. The two solid horizontal lines indicate the theoretical minimum (0.2) and maximum (0.6) F_v/F_m value for living cyanobacteria. The two vertical dashed lines indicate the temperature tolerance range of *Trichodesmium* IMS-101 (20–34°C). **(b)**: Photosynthetic quantum use efficiency of *Trichodesmium* IMS-101 grown at 25°C and exposed to the respective temperatures of F_v/F_m measurements for short duration (four hours).

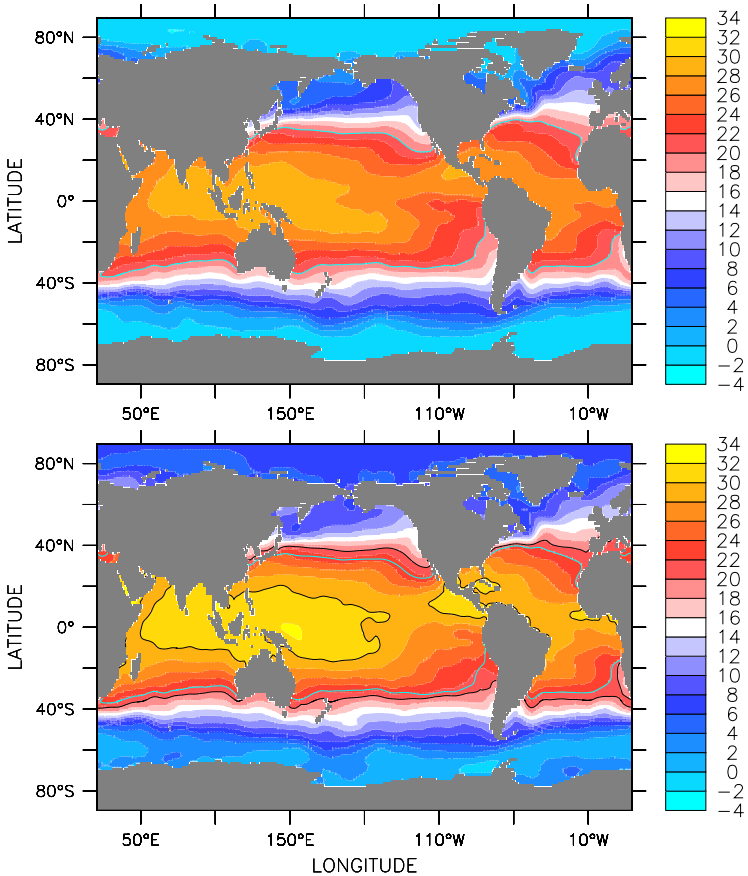

Fig. 5. The observed present-day annual mean sea surface temperature (top) in comparison to the annual mean sea surface temperature incremented by the modeled increase over the period 1990 to 2090 (bottom) based on HadCM3. In both plots, the cyan line indicates the maximum latitudinal boundary of the 20°C isotherm of the year 1990. The black lines **(b)** indicate the 20 and 30°C isotherms for the year 2090.