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Effects of warming and eutrophication on coastal phytoplankton production

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ABSTRACT

Phytoplankton production in coastal waters influences seafood production and human health and can lead to harmful algal blooms. Water temperature and eutrophication are critical factors affecting phytoplankton production, although the combined effects of warming and nutrient changes on phytoplankton production in coastal waters are not well understood. To address this, phytoplankton production changes in natural waters were investigated using samples collected over eight months, and under 64 different initial conditions, established by combining four different water temperatures (i.e., ambient T, +2, +4, and + 6 °C), and two different nutrient conditions (i.e., non-enriched and enriched). Under the non-enriched conditions, the effect of warming on phytoplankton production was significantly positive in some months, significantly negative in others, or had no effect. However, under enriched conditions, warming affected phytoplankton production positively in all months except one, when the salinity was as low as 6.5. These results suggest that nutrient conditions can alter the effects of warming on phytoplankton production. Of several parameters, the ratio of initial nitrate concentration to chlorophyll *a* concentration [NCCA, μM (μg L^{-1})$^{-1}$] was one of the most critical factors determining the directionality of the warming effects. In laboratory experiments, when NCCA in the ambient or nutrient-enriched waters was ≥1.2, warming increased or did not change phytoplankton production with one exception; however, when NCCA was < 1.2, warming did not change or decreased production. In the time series data obtained from the coastal waters of four target countries, when NCCA was 1.5 or more, warming increased phytoplankton production, whereas when NCCA was lower than 1.5, warming lowered phytoplankton production, Thus, it is suggested that NCCA could be used as an index for predicting future phytoplankton production changes in coastal waters.

1. Introduction

Phytoplankton are an essential component of coastal ecosystems, and serve as important prey for zooplankton, and diverse commercially important marine animals (Barton et al., 2013; Franks et al., 2013; Johnson et al., 2013; Lee et al., 2017). However, they sometimes proliferate into harmful algal blooms, causing heavy losses to the coastal aquaculture and tourism industries (Anderson, 1995; Harvey and Menden-Deuer, 2012; Tillmann et al., 2016; Lee et al., 2016; Gobler et al., 2017). Thus, assessing phytoplankton production – and its change – in coastal waters, is an important aspect of coastal management.

Coastal waters are important to humans because most seafood harvesting, aquaculture, water supply activities, and human recreation occur there (Canuel et al., 2012; Bianchi et al., 2013). In addition, coastal waters are likely to be affected more than open ocean waters by changes in air temperature and nutrient input from land, due to their relatively small size and restricted circulation (Kang et al., 2013). Thus it might be expected that the effects of water temperature and nutrient concentration changes on species composition and production of phytoplankton in coastal waters would be greater than those in oceanic waters.

Global warming has increased seawater temperature (e.g., Boyd

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Table 1
Sampling and initial conditions.

Y/M	T	S	Initial concentrations of nutrients and Chl *a* under the non-enriched condition (± SE)					Initial concentrations of nutrients and Chl *a* under the enriched condition (± SE)				
			NO_3	NH_4	PO_4	SiO_2	Chl *a*	NO_3	NH_4	PO_4	SiO_2	Chl *a*
2011 03	4.3	26.1	26.7 (0.9)	24.3 (0.3)	0.03 (0.01)	4.7 (0.1)	6.9 (0.3)	235.9 (10.2)	14.4 (1.2)	15.7 (0.5)	84.4 (4.2)	7.4 (0.3)
2011 04	10.5	28.8	16.8 (0.2)	7.1 (0.3)	0.01 (0.01)	1.1 (0.2)	5.7 (0.5)	193.7 (0.3)	5.9 (0.1)	12.3 (0.0)	86.8 (0.7)	3.5 (0.3)
2011 05	19.0	24.2	16.6 (0.1)	6.6 (0.2)	0.00 (0.00)	3.3 (0.1)	10.3 (0.6)	175.0 (0.9)	7.1 (0.4)	10.8 (0.1)	110.0 (1.8)	9.3 (0.6)
2011 07	26.8	6.5	106.7 (0.4)	11.5 (0.7)	0.00 (0.00)	76.5 (0.6)	61.8 (1.4)	202.8 (0.4)	7.6 (0.3)	8.2 (0.2)	99.7 (0.5)	65.7 (0.8)
2011 08	27.0	15.0	48.7 (0.8)	11.9 (0.3)	0.10 (0.02)	63.7 (0.1)	12.9 (0.5)	197.5 (4.3)	11.1 (0.7)	14.5 (0.1)	97.7 (0.7)	13.5 (0.4)
2011 10	15.3	22.8	25.4 (0.2)	38.4 (0.6)	0.47 (0.02)	11.1 (0.1)	21.5 (0.5)	174.3 (2.5)	38.1 (1.0)	12.6 (0.1)	91.3 (0.5)	22.6 (0.4)
2011 12	7.0	28.0	13.1 (0.1)	0.6 (0.0)	0.06 (0.01)	1.1 (0.0)	25.4 (0.2)	211.6 (0.7)	0.6 (0.0)	12.9 (0.1)	95.3 (0.9)	23.3 (0.5)
2012 01	0.2	31.1	0.04 (0.04)	0.7 (0.0)	0.03 (0.01)	0.0 (0.0)	103.3 (0.5)	168.0 (2.2)	0.7 (0.0)	12.6 (0.2)	103.4 (1.1)	96.8 (1.7)

Sampling and initial conditions. Sampling year and month (Y / M), water temperature (T, °C) and salinity (S) in the collected waters; initial nutrients (NO_3, NH_4, PO_4, SiO_2, μM), and Chlorophyll *a* (Chl *a*, μg L^{-1}), at the beginning of the incubation experiments.

et al., 2015). Furthermore, many models have predicted an increase in global temperature in a range of 2–6 °C in the next 100 years (IPCC, 2013), with consequent increases in seawater temperatures. Nutrient conditions in a country's coastal waters can vary depending on its policies regarding the use of sewage or wastewater treatment technologies, on fertilizer application, on precipitation patterns, and on freshwater discharge (Howarth, 2008). Thus, ecosystems in coastal environments experience changes in both water temperature and nutrient conditions (Scavia et al., 2002; O'Neil et al., 2012; Wells et al., 2015; Burkholder et al., 2018). Several studies have examined the effects of warming or nutrient changes on phytoplankton production, but only a few have focused on their combined effects (Calbet et al., 2014; Lewandowska et al., 2014). To understand and predict changes in phytoplankton production and assist the beneficial management of coastal environments, the combined effects of changes in seawater temperature and nutrients should be explored.

To address the effects of warming and nutrient conditions on phytoplankton production in coastal waters, water samples were collected from a shallow Korean bay, on eight occasions from March 2011 to January 2012. These samples were incubated under eight different conditions, using four different water temperatures (ambient T, T + 2, T + 4, and T + 6 °C), and two nutrient conditions (non-enriched (NE) and enriched (ER)). Then the phytoplankton biomass - as chlorophyll *a* (Chl *a*) concentrations - and nutrient concentrations were monitored daily for 7 days. Furthermore, to test a possibility that these study results were applicable to other marine environments, time series data on water temperature, nutrient concentrations, and Chl *a* concentrations in waters of the UK, Norway, Estonia, and USA (California) were analyzed, and their trends were compared with the results presented here.

The results of the present study provide a basis for understanding both the independent and combined effects of warming and eutrophication on coastal phytoplankton production, and also on the dynamics of harmful algal blooms.

2. Materials and methods

2.1. Sampling system and establishment of experimental procedure

Surface water samples of 400 L were collected from a sampling site (SWSNU) in Shiwha Bay, Korea, in March, April, May, July, August, October, and December 2011, and January 2012 (Table 1 and Fig. 1). Temperature and salinity of the seawater samples were measured using YSI 63 instruments (YSI, Yellow Springs, OH, USA) as soon as the samples were collected. The collected seawater samples were immediately transported to the laboratory, and zooplankton were screened out with a 200 μm sieve.

The concentrations of ammonia (NH_4), nitrite plus nitrate (reported as nitrate or NO_3 in this paper), phosphate (PO_4), and silicate (SiO_2) in the seawater samples were measured using a 2-channel, nutrient autoanalyzer (QuAAtro, SEAL analytical GmbH, Germany). Then, the seawater samples were gently mixed and evenly distributed into 24 × 10 L transparent polycarbonate (PC) bottles (Nalgene, Rochester, New York, USA), and maintained for approximately 12 h at ambient temperature inside two different temperature-controlled chambers. Selected samples were enriched (ER) with the addition of predetermined amounts of NO_3, PO_4, and SiO_2 to 12 × 10 L PC bottles to reach final / target concentrations of approximately 200 μM for NO_3, 12 μM for PO_4 (N : P = 16 : 1, Redfield, 1958), and 100 μM for SiO_2. The NO_3 concentrations of the samples corresponded with the maximum corresponding concentrations observed in the major rivers of the world (Turner et al., 2003). Trace metals and vitamins were also added, based on the f/2 medium (Guillard and Ryther, 1962). The water in the other 12 × 10 L PC bottles remained as NE (i.e., the nutrient concentrations were the same as those of the ambient water).

Triplicate ER bottles and triplicate NE bottles were placed inside one of the four different temperature-controlled chambers for the ambient water temperature (T) experiment. In the same manner, triplicate ER and triplicate NE bottles were set up for each temperature elevation for the experiments at 2 °C (T + 2 °C), 4 °C (T + 4 °C), and 6 °C (T + 6 °C). All bottles were capped loosely, placed inside one of the four different temperature-controlled chambers, and then incubated at the target temperature under an illumination of 50 μE m^{-2} s^{-1}, provided by a cool white fluorescent light, in a 14:10 h light–dark cycle.

2.2. Subsampling and component analyses

Daily aliquots of 500 mL were taken from each of the 24 bottles. For the Chl *a* analysis, a 100 mL aliquot (50 mL aliquot when a bloom

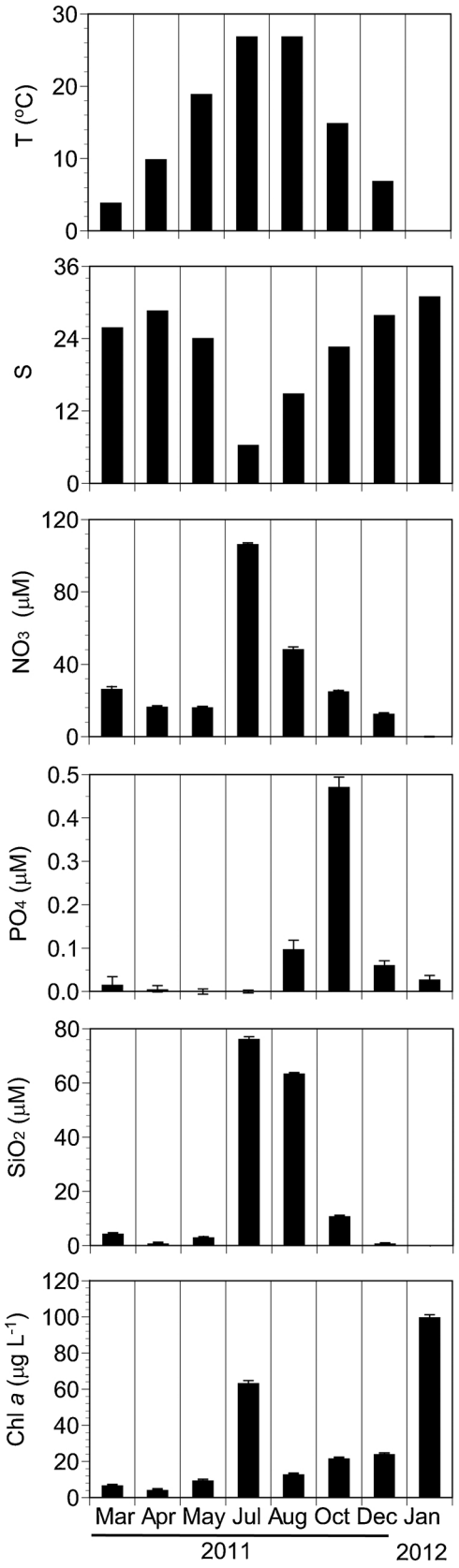

Fig. 1. Physical and chemical properties and Chl *a* concentrations in the sampled waters. Temporal variations in temperature (T), salinity (S), and concentrations of nitrate (NO_3), phosphate (PO_4), silicate (SiO_2), and Chl *a* in surface water samples from Shiwha Bay, Korea, over March 2011–January 2012. Symbols represent treatment means ± 1 SE.

occurred) from each bottle was gently filtered through a GF/F filter, and the filter paper was placed in a 15 mL Falcon tube. A 10 mL volume of 90% acetone was added to the tube, which was then sonicated for 10 min, before being placed in a dark chamber at 4 ˚C for one night. The samples were then centrifuged and the supernatant was carefully taken for Chl *a* measurement, using a 10-AU Turner fluorometer (Turner Designs, Sunnyvale, CA, USA). For nutrient analysis, 20 mL aliquots from each bottle were placed in a high-density polyethylene container, after filtering through GF/F. The concentrations of NO_3 and PO_4 were determined daily, using a 2-channel, nutrient auto-analyzer (QuAAtro, SEAL analytical GmbH, Germany).

For the determination of plankton abundance, a 20 mL aliquot was taken daily from each bottle and fixed with Lugol's acid solution. Phytoplankton at the beginning of the experiment were enumerated in a Sedgwick–Rafter chamber by counting > 200 cells or all for each species in ×50–200 using light microscopy (BX51, Olympus, Japan).

2.3. Data analysis

The Chl *a* concentration in each bottle was measured daily. To compare the chl *a* concentrations among the treatments, integrated Chl *a* concentrations [$Chl_{Int(t=0\text{-}7d)}$ and $Chl_{Int(t=1\text{-}7d)}$ (μg/L)] were calculated:

$$Chl_{Int(t=0-7d)} = \sum_{t=0}^{7} Chl_{(t)} \quad (1)$$

$$Chl_{Int(t=1-7d)} = \sum_{t=0}^{7} Chl_{(t)} - Chl_{(t=0d)} \quad (2)$$

In Eqs. (1) and (2), $Chl_{(t)}$ is the Chl *a* concentration for the elapsed day, and t the number of elapsed days (0–7 d).

Using *P* for phytoplankton (in nitrogen units), and μ for the phytoplankton intrinsic growth rate, the change in the phytoplankton concentration over time (*t*) can be modeled using the logistic equation:

$$\frac{dP}{dt} = \mu P\left(1 - \frac{P}{N_0}\right)$$

where it is assumed that the carrying capacity N_0 is given by the initial nutrient concentration. The solution to this is

$$P(t) = \frac{N_0}{1 + \left(\frac{N_0}{P_0} - 1\right)e^{-\mu t}}$$

where P_0 is the initial phytoplankton concentration. The ratio of the final phytoplankton concentration to the initial phytoplankton concentration is

$$\frac{P(t)}{P_0} = \frac{N_0}{P_0}\left(1 + \left(\frac{N_0}{P_0} - 1\right)e^{-\mu t}\right)^{-1}$$

When μt is large (i.e., after several cell divisions), this reduces to

$$\frac{P(t)}{P_0} = \frac{N_0}{P_0}$$

Thus the ratio of the initial concentrations of nutrient and phytoplankton (right hand side of the preceding equation) gives the ratio of the final and initial phytoplankton concentrations – that is, the relative magnitude of a phytoplankton bloom. This result can be related to the field and laboratory measurements by using the initial measured concentration of NO_3 divided by the initial measured concentration of Chl *a*. This ratio is defined as the NCCA (nitrate concentration to chlorophyll *a*). This ratio should correspond to the ratio of the magnitude of the potential phytoplankton bloom to the initial phytoplankton concentration, as shown by the analyses above. A PCCA can be similarly

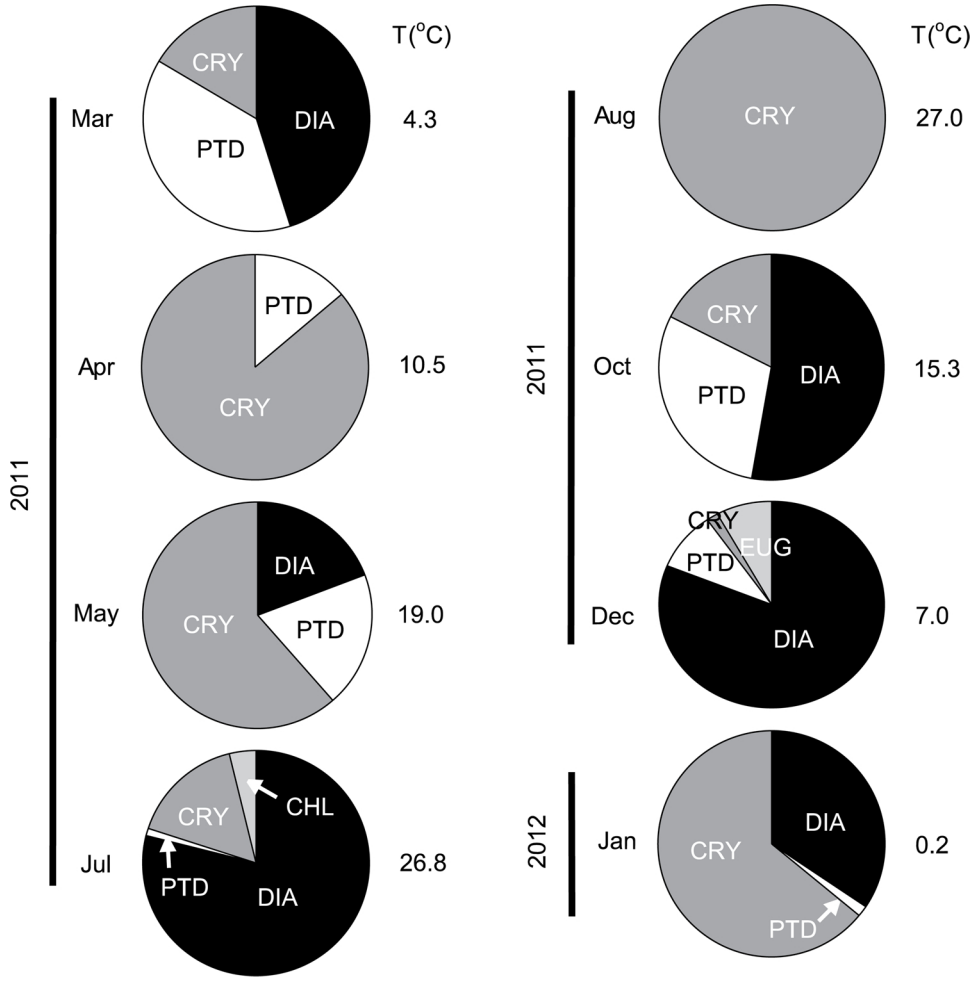

Fig. 2. Ratio of the abundances of the initial dominant phytoplankton groups in the sampled waters. Ratio (%) of the abundances of the five most dominant phytoplankton groups in the water samples collected from Shiwha Bay from March 2011–January 2012. T = initial water temperature (°C); PTD = phototrophic dinoflagellates; DIA = diatoms; CRY = cryptophytes; CHL = chlorophytes; EUG = euglenophytes.

defined as the ratio of the concentrations of PO_4 relative to that of Chl *a*. The NCCA and PCCA can be thus used as indicators of the potential for phytoplankton blooms.

2.4. Statistical analysis

The *t*-test (Zar, 1999) was used to test whether the $Chl_{Int(t=1\text{-}7d)}$ of one treatment was higher or lower than that of the control (i.e., T under NE condition) for each month. In addition, linear regression ANOVA analyses were performed (using IBM SPSS Statistics 23 (IBM Corp., New York, USA)) to test whether $Chl_{Int(t=1\text{-}7d)}$ was affected by the degree of water temperature increase.

2.5. Environmental data analysis

To apply our study results and predict trends, data on water temperature, NO_3 concentrations, and Chl *a* concentrations in the waters of the UK (in 2000–2012), Norway (2000–2012), Estonia (2000–2012), and the USA (California) (2005–2012) were analyzed. To discern a trend in Californian waters, downcast CTD data were obtained from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) website (http://calcofi.org/) for 2005–2012 (excluding 2008). Data from 0 to 3 m depth were used in this analysis.

For identifying trends in the waters of the UK, Norway, and Estonia, data provided by the European Environmental Agency from 2000 to 2012, were obtained from its website (https://www.eea.europa.eu/). Data from 0 to 20 m depth for the UK and Estonian waters were used in this analysis, and the corresponding depth for Norwegian waters was 0–5 m. Linear regression ANOVA analyses were performed as described above.

3. Results

3.1. Physical, chemical, and biological properties of the ambient and experimental waters

During the study period, the major environmental parameters - water temperature, salinity, nutrient concentration, and Chl *a*

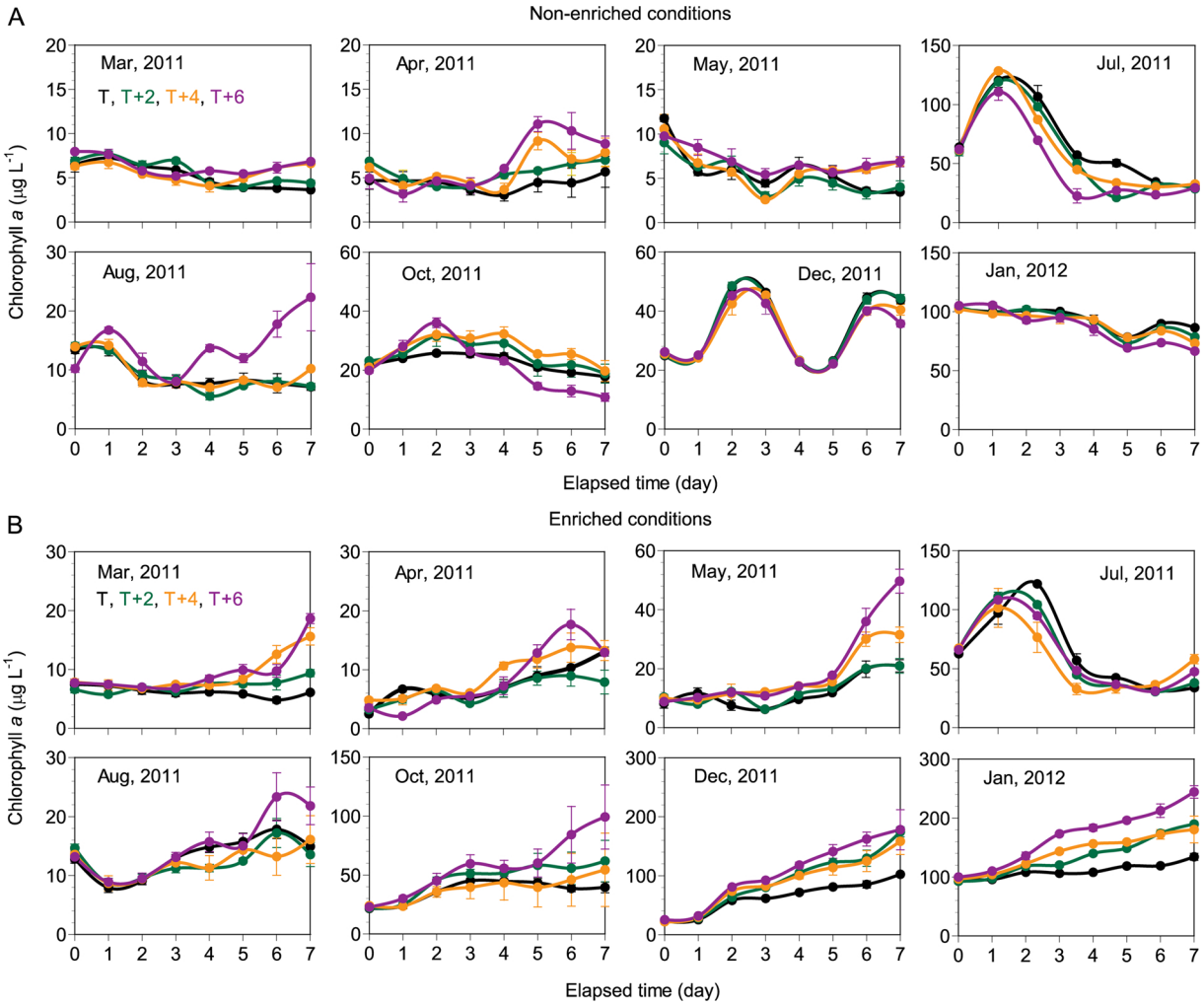

Fig. 3. Daily variations in the Chl *a* concentrations (μg L^{-1}) in each month. Non-enriched conditions (A); Enriched conditions (B). Symbols represent treatment means ± 1 SE.

concentration - showed wide ranges (Table 1 and Fig. 1). The ambient water temperature ranged from 0.2 to 27 °C, while salinity ranged between 6.5–31.1 (Table 1 and Fig. 1). Furthermore, the nutrient concentrations of the sampled waters ranged from 0.04 to 106.7 μM for NO_3, 0.6–38.4 μM for NH_4, 0–0.5 μM for PO_4, and 0.02–76.5 μM for SiO_2 (Table 1 and Fig. 1). The Chl *a* concentrations ranged between 3.5–103.3 μg L^{-1} (Table 1 and Fig. 1).

The three most dominant phytoplankton groups at the beginning of the experiments were diatoms, phototrophic dinoflagellates, and cryptophytes (Fig. 2). The dominant phototrophic dinoflagellates were *Heterocapsa rotundata, Heterocapsa steinii* (*H. triquetra*), *Prorocentrum cordatum* (*P. minimum*), and *Prorocentrum micans*, while the dominant diatoms were *Chaetoceros* spp., *Nitzschia* spp., *Stephanodiscus hantzschii*, *Thalassiosira* spp., and unidentified diatoms. However, the dominant cryptophytes, chlorophytes, and euglenophytes could not be identified to species level using the available microscopy, because of their small sizes and similar morphological characteristics.

3.2. Nutrient concentration changes during incubation

Under the NE conditions, compared to Day 0, the concentrations of NO_3 at Day 7 decreased in some months, and did not significantly change in other months, whereas under ER conditions, those at Day 7 decreased in most months (Fig. S1). The final concentrations of NO_3 at Day 7 were > 10 μM for all months, except for December 2011 and January 2012 under the NE conditions (Fig. S1). Furthermore, under the NE conditions, the concentrations of PO_4 at Day 0 were as low as < 0.6 μM, but increased to 1.7 μM at the end of the experiment (Fig. S2). However, under the ER conditions, the concentrations of PO_4 between Day 0 and Day 7 decreased in all months, except for July 2011 (Fig. S2). The final concentrations of PO_4 at Day 7 were > 2 μM in all months under the ER conditions (Fig. S2).

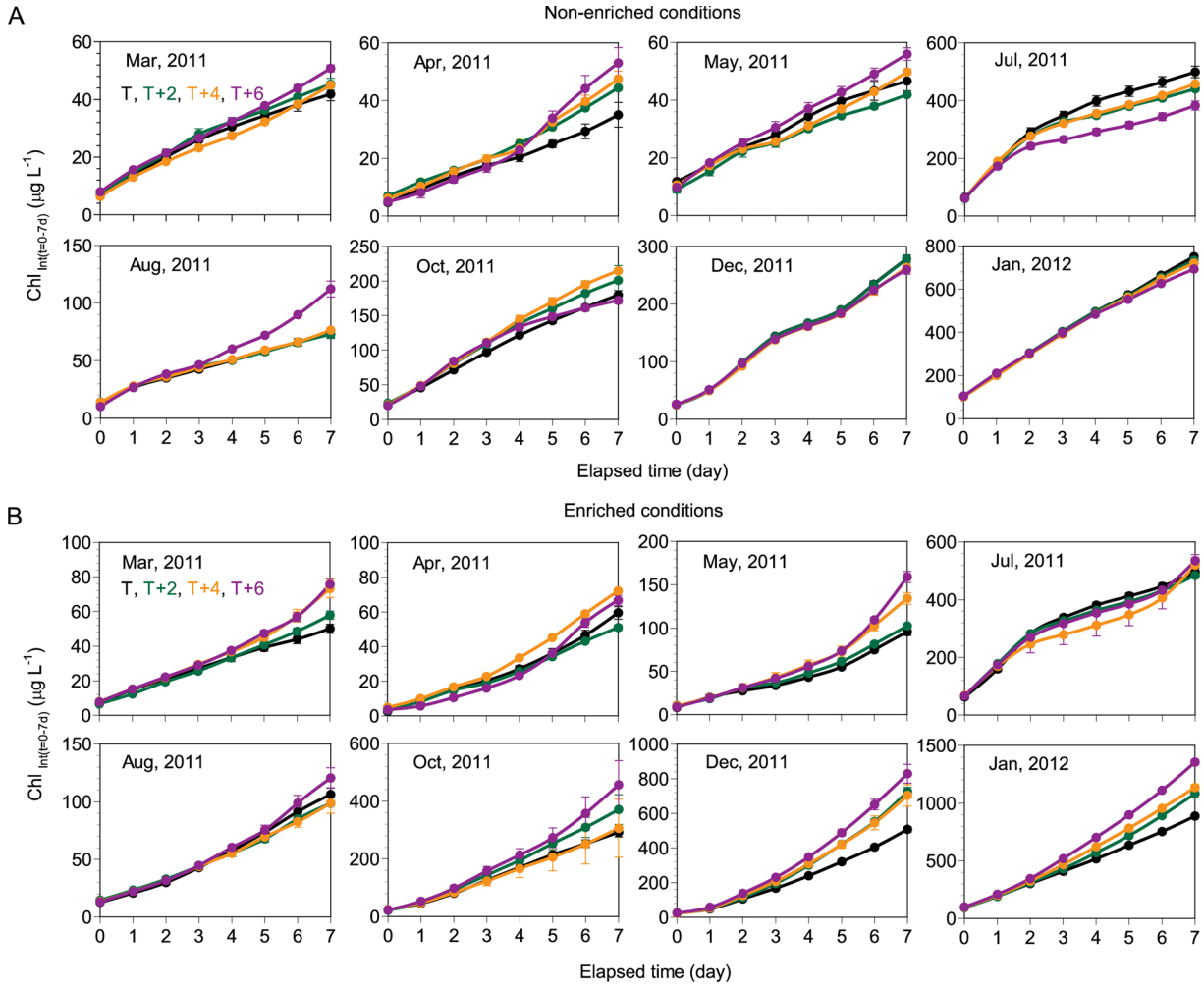

Fig. 4. Daily variations in the integrated Chl *a* concentrations [$Chl_{Int(t=0\text{-}7d)}$, (μg L^{-1})] in each month. Non-enriched conditions (A); Enriched conditions (B). Symbols represent treatment means ± 1 SE.

3.3. Chlorophyll a concentration changes during incubation

Under NE conditions, compared to Day 0, the Chl *a* concentration at Day 7 increased, decreased, or did not significantly change, whereas under ER conditions, those at Day 7 increased in all months except for July 2011 (Fig. 3).

Under the NE conditions, at Day 7, compared to the $Chl_{Int(t=1\text{-}7d)}$ concentrations at T °C, those at T + 2 °C, T + 4 °C, and T + 6 °C were higher, lower, or similar, whereas under ER conditions, those at T + 2 °C, T + 4 °C, and T + 6 °C were almost always higher (Fig. 4).

3.4. Effects of elevated temperature

Under the NE condition, the $Chl_{Int(t=1\text{-}7d)}$ concentrations at T + 2 °C, T + 4 °C, or T + 6 °C were significantly higher than those at T °C from March to October 2011, except for July, but significantly lower July 2011 and January 2012 ($p < 0.05$, *t*-test; Fig. 5).

Under the NE condition, with increasingly elevated T, the difference between $Chl_{Int(t=1\text{-}7d)}$ at T °C and at the elevated T (T + 2 °C, T + 4 °C, or T + 6 °C) significantly increased in March, April, May, and August 2011 ($p < 0.01$, ANOVA; Fig. 5), but significantly decreased in July and December 2011 and January 2012 ($p < 0.05$, ANOVA; Fig. 5).

In these experiments, the initial concentrations of NO_3 were generally > 13 μM, except in January 2012 (0.04 μM), but initial concentrations of PO_4 were generally ≤ 0.1 μM, except in October 2011 (0.47 μM) (Fig. 5).

3.5. Effects of nutrient enrichment

The $Chl_{Int(t=1\text{-}7d)}$ concentration at T °C under the ER condition was significantly higher than at T °C under the NE condition, in all months, except for July 2011 ($p < 0.05$, *t*-test; Fig. 6).

In these experiments, the initial concentrations of NO_3 and PO_4 ranged from 168.0 to 235.9 μM and from 8.2 to 15.7 μM, respectively

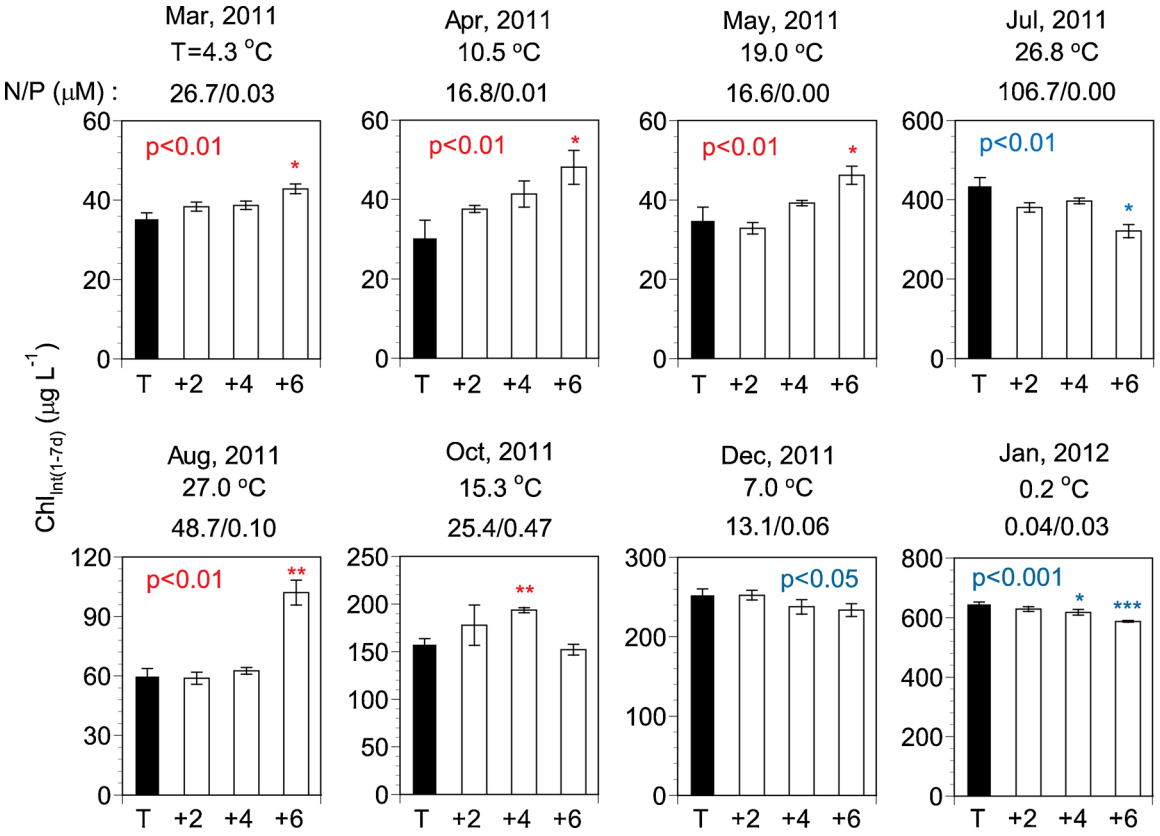

Fig. 5. Warming effects. Comparison of $Chl_{Int(t=1\text{-}7d)}$ under the control (T °C), and experimental (T + 2, T + 4, and T + 6 °C) conditions, and significance of the differences. T = sample water temperature for each sampling month; N / P (μM) = initial concentrations of NO_3 and PO_4 under NE conditions; red stars indicate an increase, and blue stars indicate a decrease compared to the control (unaltered) conditions (*t*-test). *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. The red and blue p-values indicate increase and decrease linear regression results (ANOVA). Symbols represent treatment means ± 1 SE.

(Fig. 6).

3.6. Combined effects of warming and nutrient enrichment

The $Chl_{Int(t=1\text{-}7d)}$ concentrations at T + 2 °C, T + 4 °C, and T + 6 °C, under the ER condition, were significantly higher than those at T °C under the NE condition in all sampling months except July 2011 ($p < 0.05$, *t*-test; Fig. 7).

Under the ER condition, with increasing elevated T, differences of $Chl_{Int(t=1\text{-}7d)}$ at T + α °C (T + 2 °C, T + 4 °C, or T + 6 °C) relative to T °C significantly increased in all months, except for July 2011 ($p < 0.05$, ANOVA; Fig. 7).

In these experiments, the initial concentrations of NO_3 and PO_4 were the same as those for experiments described in section *3.5* (Fig. 7).

3.7. Proposal of a new index for predicting phytoplankton production

Under NE conditions, the NCCA in the water samples in each month ranged from 0.0 to 5.1 (Fig. 8A). In addition, when nutrients were added (i.e., under the ER conditions), the NCCA in each month increased to range between 1.7–80.5 (Fig. 8B, 8C). Under NE conditions, with one exception (July 2011), $Chl_{Int(t=1\text{-}7d)}$ concentrations at T + α °C were significantly higher than those at T °C or not significantly different, at NCCA ≥ 1.2, but significantly lower or not significantly different, at NCCA < 1.2 (Fig. 8A, 8D). In July 2011, $Chl_{Int(t=1\text{-}7d)}$ at T + 6 °C, was significantly lower than that at T °C ($p < 0.05$, *t*-test; Fig. 8A), although NCCA was ≥ 1.2. Furthermore, with one exception (July 2011), when NCCA ≥ 1.7, $Chl_{Int(t=1\text{-}7d)}$ at T °C under the ER conditions were significantly higher than those at T °C under the NE conditions ($p < 0.05$, *t*-test; Fig. 8B, 8D). Moreover, under the ER condition, with three exceptions (all T + α °C in July and T + 4 °C in August and October 2011), when NCCA values were ≥ 1.7, $Chl_{Int(t=1\text{-}7d)}$ at T + α °C were significantly higher than those at T °C ($p < 0.05$, *t*-test; Fig. 8C, 8D).

Under NE conditions, the PCCA in the water samples in each month ranged from 0.00 to 0.02 (Fig. S3A). In addition, under the ER conditions, the PCCA in each month increased to range between 0.1–5.1 (Fig. S3B, S3C). Under the NE conditions, $Chl_{Int(t=1\text{-}7d)}$ concentrations at

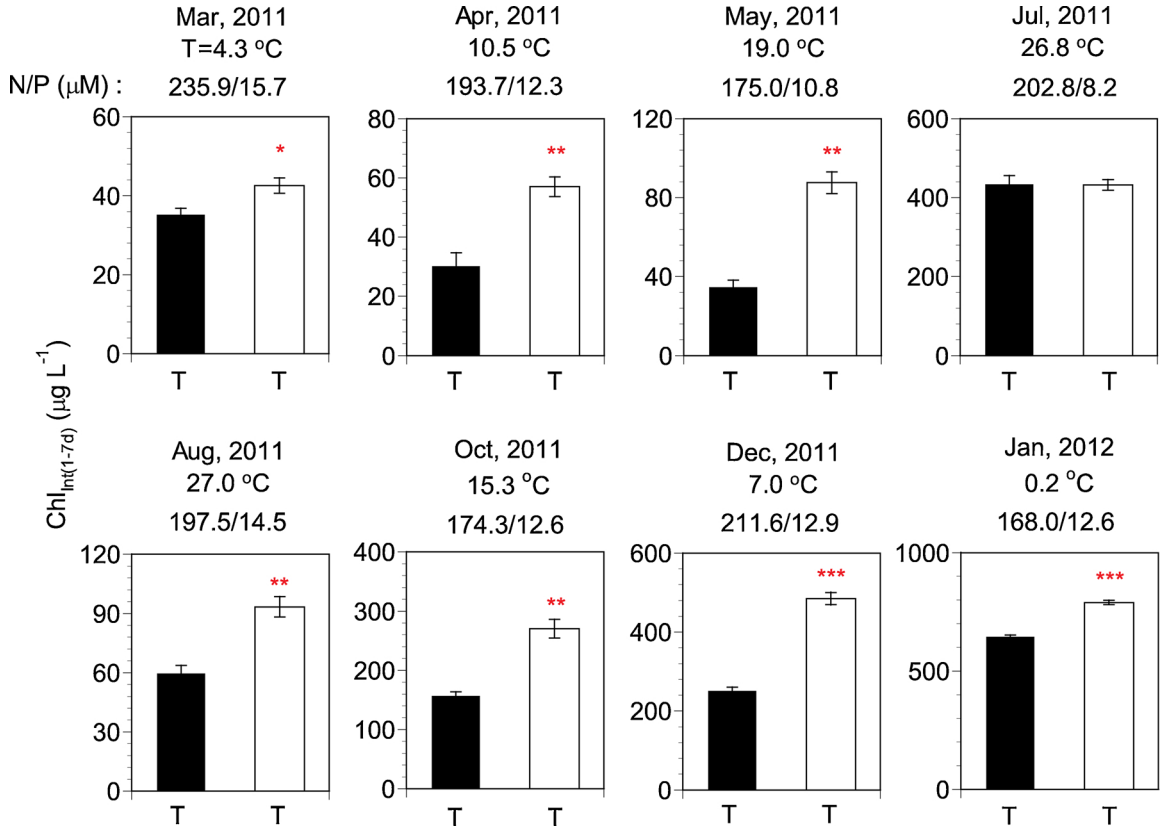

Fig. 6. Nutrient enrichment effects. Comparison of $Chl_{Int(t=1\text{-}7d)}$ under the control (NE) and experimental (ER) conditions, and significance of the differences. T = sample water temperature for each sampling month; N / P (μM) = initial concentrations of NO_3 and PO_4 under ER conditions; red stars indicate an increase compared to the control (unaltered) conditions (*t*-test). *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Symbols represent treatment means ± 1 SE.

T + α °C were significantly higher than those at T °C or not significantly different at PCCA ≥ ca. 0.005, but significantly higher, lower, or not significantly different, at PCCA < ca. 0.005 (Fig. S3A, S3D). Furthermore, with one exception (July 2011), when PCCA values were ≥ 0.12, $Chl_{Int(t=1\text{-}7d)}$ at T °C under the ER conditions were significantly higher than those at T °C under the NE conditions ($p < 0.05$, *t*-test; Fig. S3B, S3D). Under the ER condition, with three exceptions (all T + α °C in July and T + 4 °C in August and October 2011), when PCCA ≥ 0.11, $Chl_{Int(t=1\text{-}7d)}$ at T + α °C were significantly higher than those at T °C ($p < 0.05$, *t*-test; Fig. S3C, S3D).

3.8. Applying NCCA critical value to world environments

To test whether the critical value NCCA ~1.5 (average of 1.2 and 1.7 = 1.45 = ~1.5, as mentioned above) was applicable to other coastal and marine waters, temporal variations in water temperature, NCCA, and Chl *a* concentration in the waters of the UK (in 2000–2012), Norway (2000–2012), Estonia (2000–2012), and USA (California) (2005–2012) were analyzed. The water temperatures for the UK, Norway, and Estonia significantly increased (Fig. 9 A–C), whereas those for California did not change significantly (Fig. 9D). However, the Chl *a* concentrations in the UK significantly increased (Fig. 9A), but those in Norway, Estonia, and California significantly decreased (Fig. 9B–D). NCCA values typically exceeded 1.5 in the UK, but were less than 1.5 in Norway, Estonia, and California.

4. Discussion

Although many models have been used to predict the effects of global warming or nutrient enrichment on phytoplankton production (Bopp et al., 2001; Sarmiento et al., 2004; Gregg et al., 2005; Marinov et al., 2010; Steinacher et al., 2010), measured values of critical parameters for the models are lacking. This is because there have been few enclosure studies that acquired values and trends for the parameters deemed important here (Sommer and Lengfellner, 2008; Lassen et al., 2010; Sommer and Lewandowska, 2011; Calbet et al., 2014; Lewandowska et al., 2014). Furthermore, only two studies have examined the combined effects of global warming and nutrient enrichment on phytoplankton production using enclosures (Calbet et al., 2014; Lewandowska et al., 2014). However, these studies explored the combined effects under single initial temperatures; the initial and changed temperatures were 11 °C and –3 and + 3 °C, or 12.3 °C

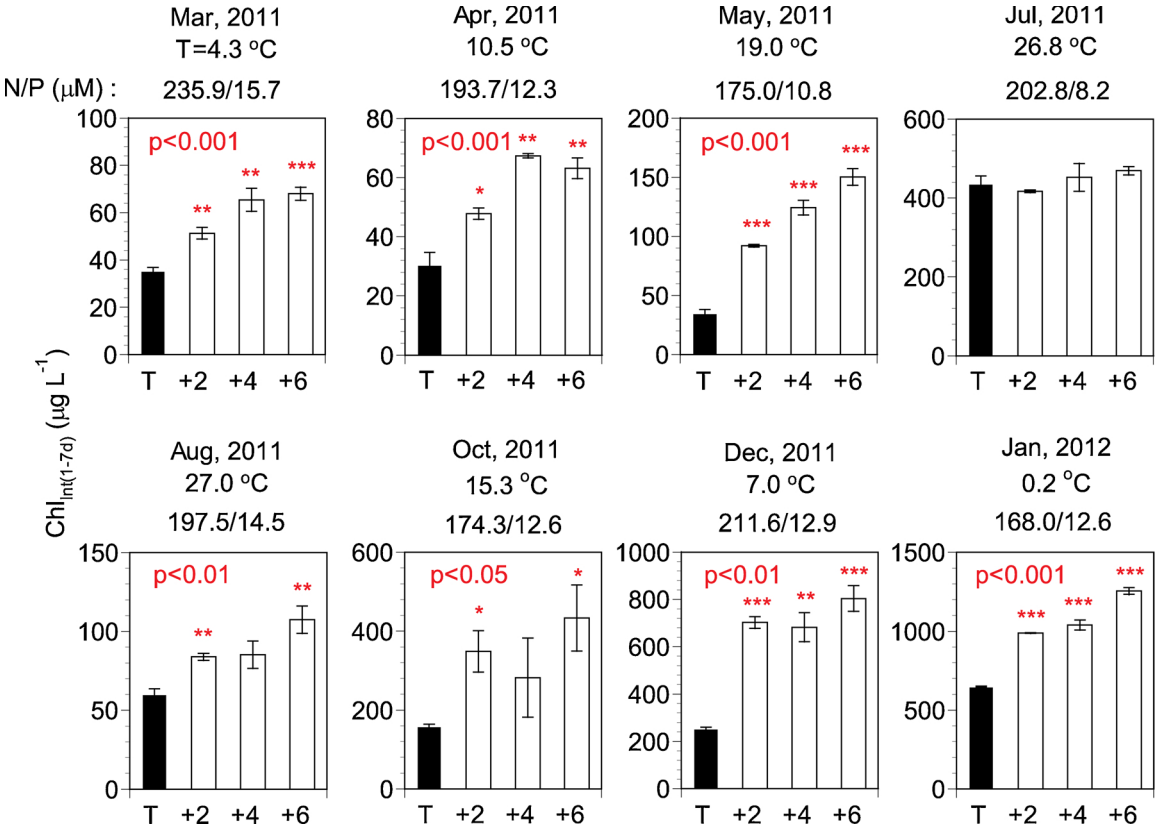

Fig. 7. Combined effects. Comparison of $Chl_{Int(t=1\text{-}7d)}$ under the control (T °C under NE condition) and experimental (T + 2, T + 4, and T + 6 °C under ER conditions) conditions, and significance of the differences. T = the temperature in the waters collected in each month; N / P (μM) = initial concentrations of NO_3 and PO_4 under the enriched conditions; red stars indicate an increase compared to the control (unaltered) conditions (*t*-test). *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. The red and blue p-values indicate increase and decrease linear regression results (ANOVA). Symbols represent treatment means ± 1 SE.

and +3 °C, respectively. Furthermore, NO_3 concentrations of the ambient waters under NE and ER conditions were 0.11 and 0.12–0.14 μM, and ~0.9 and ~11–14 μM, respectively. However, the range of water temperatures in global coastal waters is – 8 to 35 °C (Alaska and Pacific coastal), and that of NO_3 is 0–200 μM (NOAA, 2018; Cloern, 2001; Zhou et al., 2008; Hayn et al., 2014). In this study, the initial temperatures and NO_3 concentrations in the ambient seawaters were 0.2–27 °C and 0–107 μM, respectively, and elevated water temperature and enriched NO_3 concentrations tested were 2.2–33 °C and 168–236 μM, respectively. Thus, the ranges of 0.2–33 °C and 0–236 μM (NO_3) in this study cover those in most coastal environments at present, and also cover the likely changes forecast for the future. Therefore, to better understand the combined effects of warmer temperatures and eutrophication on phytoplankton production, experiments using phytoplankton populations collected from natural environments, in a wider range of water temperatures and nutrient concentrations, should be conducted.

4.1. Effect of elevated temperature and nutrient enrichment on phytoplankton production

In March, April, May, August, October, and December 2011, $Chl_{Int(t=1\text{-}7d)}$, under the NE conditions, was not affected by elevated water temperature at two or three T + α °C, but became positively affected by elevation of water temperature under ER conditions. Furthermore, in January 2012, $Chl_{Int(t=1\text{-}7d)}$, under the NE conditions, was negatively affected by elevation of water temperature, but became positively affected by elevation of water temperature under ER conditions. These results indicated that the effect of elevated water temperature on phytoplankton production was influenced by nutrient levels – and this is believed to be the first study showing that nutrients influence the effect warming has on phytoplankton production. Moreover, $Chl_{Int(t=1\text{-}7d)}$ under both NE and ER conditions were affected by the degree of water temperature elevation in seven out of eight months. Therefore, $Chl_{Int(t=1\text{-}7d)}$ is generally affected by the degree of elevation of water temperature.

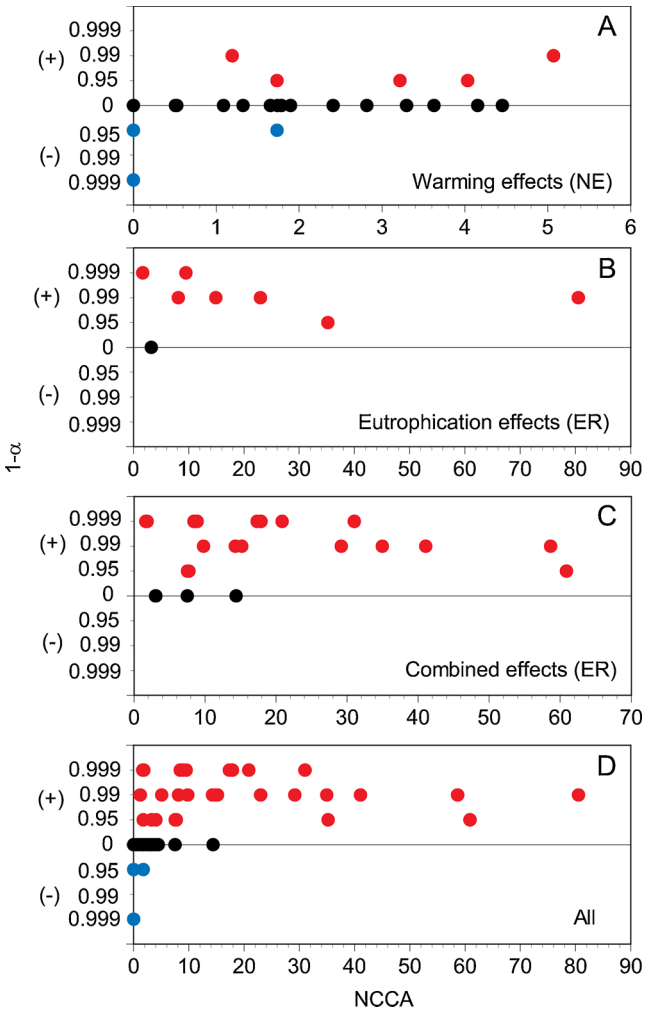

Fig. 8. Significance of the differences (i.e., effects; 1-α) in $Chl_{Int(t=1\text{-}7d)}$ between the control (T and NE) and experimental conditions (combination of T + 2, T + 4, or T + 6 ˚C and / or ER) as a function of the initial ratios of NO_3 concentration to Chl *a* concentration (NCCA). α: Significance level. The blue circles indicate negative effects; the black circles indicate no effects; red circles indicate positive effects; (A) Warming effects only; (B) Nutrient enrichment effects only; (C) Combined effects of warming and nutrient enrichment; (D) All.

In the effects of nutrient enrichment on the $Chl_{Int(t=1\text{-}7d)}$ concentration, the results in July 2011 were exceptional. The salinity in the waters collected in this month was as low as 6.5. This salinity is lower than the salinity limits for a positive growth of many marine phytoplankton species (Brand, 1984; Jeong et al., 2018). Therefore, low salinity in July 2011 may explain why these data are outliers.

4.2. Nutrient concentration effects

The dynamics of the major nutrients N, P, and Si, in coastal waters, are known to be affected by freshwater input, seasonal dynamics, and regional characteristics (Trommer et al., 2013; Maavara et al., 2015; Jeong et al., 2017). Eutrophic waters are usually favorable for algal blooms (Glibert et al., 2005a, 2005b). In general, marine environments are considered to be N-limited for phytoplankton growth, whereas lakes are P-limited (Rabalais et al., 2002; Howarth and Marino, 2006). However, in some coastal regions, seasonally, P is a limiting nutrient (Fisher et al., 1992; Rabalais et al., 2002; Trommer et al., 2013). Furthermore, P as well as N are also known to affect dynamics of algal blooms in many waters, thus, ideas for controlling N and / or P to prevent algal blooms have been suggested (Ryther and Dunstan, 1971; Smith, 2006; Elser et al., 2007; Paerl et al., 2016; Jeong et al., 2017).

In this study period, the PO_4 concentrations in the waters collected for eight months were as low as 0.00–0.47 μM, however, Chl *a* increased in some months at T or T + α ˚C. Though it did not appear to explain the trends in our data, PO_4 or PCCA may affect changes in Chl *a* in other regions, and it is therefore worthwhile exploring this relationship in other regions.

4.3. Applying an NCCA critical value to world environments

A criterion for the conditions under which nutrient enrichment alters the results of rising water temperature on phytoplankton is needed. In this study, NCCA – the ratio of nitrate concentration to chlorophyll *a* – was chosen as a potential criterion. When combining the data obtained under NE and ER conditions, NCCA values of 1.2–1.7 were found to be critical values for predicting the combined influence of nutrients and rising temperatures had on phytoplankton production.

When trends in Chl *a* concentration in the waters of the UK, Norway, Estonia (Baltic), and USA (California) were analyzed, increases in Chl *a* concentrations were largely explained by whether NCCA exceeded 1.5 or not – evidence that supports the adoption of NCCA as a criterion. Furthermore, if the UK, Norway, Estonia, and USA were to maintain their respective NCCA trends for the values recorded for 2000 or 2005–2012, phytoplankton production in UK waters would increase, while that in Norway, Estonia, and California (USA) would decrease. Our prediction method should be applicable to other regions.

Many studies have predicted that rising water temperatures will lower phytoplankton biomass in the future, because stronger thermoclines would limit mixing between oligotrophic surface waters and eutrophic deep waters, consequently lowering the nutrient flux in surface waters (Behrenfeld et al., 2006, 2015; Doney, 2006; Boyce et al., 2010). This prediction does not however consider changes in nutrient concentrations in coastal environments and, according to the results of a recent study analyzing 50 years of data, increased phytoplankton production caused by rising seawater temperature in the North Atlantic subpolar region, due to increased nutrient concentrations from a deepened thermocline depth, was suggested (Martinez et al., 2016).

The results of this study suggest that nutrient conditions - NCCA rather than absolute concentration - influence the effects of warming on phytoplankton. It is therefore suggested that the effects of NCCA should be considered when running prediction models for phytoplankton dynamics in warmer and / or eutrophic seawater conditions.

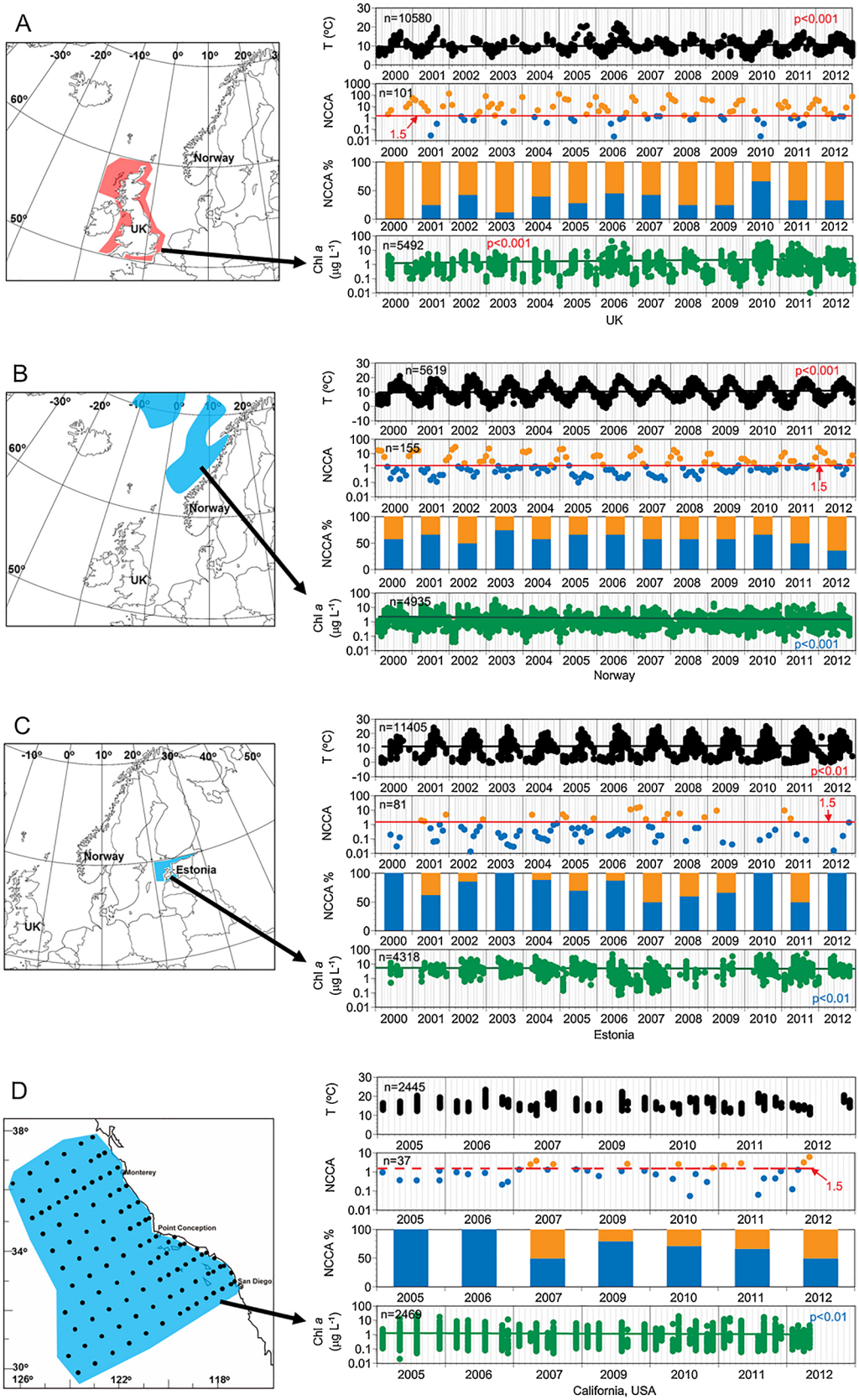

Fig. 9. Trends in water temperature (T), NCCA, ratio of NCCA ≥ 1.5 relative to < 1.5, and Chl *a* concentration in the waters of 4 target countries where algal blooms occur; NCCA indicates ratios of NO_3 concentration to Chl *a* concentration; blue bars indicate NCCA < 1.5, while the orange bars denote NCCA ≥ 1.5; sampling periods for the UK (A), Norway (B), and Estonia (C) ranged from 2000 to 2012, while that for USA (California) was from 2005 to 2012 (D); n indicates the number of samples analyzed; p-values from the ANOVA linear regression test indicate a significant increase (red color) or decrease (blue color); the red line indicates NCCA = 1.5.

Conflict of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.hal.2018.11.017.

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