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NOTES AND CORRESPONDENCE

Relationship of *Synechococcus* Abundance to Seasonal Ocean Temperature Ranges

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ABSTRACT

The abundance of *Synechococcus* in the East China Sea (ECS) was tracked during two sets of cruises in 1997 - 1998 and 2004. These data were combined with information from the literature to examine the hypothesis wherein variations in *Synechococcus* abundance were linked to the magnitude of seasonal temperature ranges. An index of the amplitude of *Synechococcus* seasonal abundance relative to their minimum abundance ($\Delta N/N_{min}$) was well correlated with the range of sea surface temperature (ΔT). These results suggest that the regional range of temperature is a relatively good predictor for the relative seasonal change in *Synechococcus* abundance within many environments.

Key words: East China Sea, *Synechococcus*, Seasonal variations, Temperature, Temperate oceans

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1. INTRODUCTION

Picophytoplankton, predominantly *Synechococcus* and *Prochlorococcus*, are widely distributed throughout the world's oceans and are responsible for an important fraction of primary productivity especially in nutrient-poor waters (Olson et al. 1990; Legendre and Rassoulzadegan 1996; Agawin et al. 2000; Chiang et al. 2002; Worden et al. 2004). In oligotrophic waters, *Synechococcus* are most abundant in surface waters, whereas the eukaryotic *Prochlorococcus* appear to create a deeper subsurface biomass maximum (Goericke et al. 2000). Several seasonal studies of *Synechococcus* distribution found maximum abundance during warmer months, during which *Synechococcus* contributed significantly to total phytoplankton biomass and production (Waterbury et al. 1986; Agawin et al. 1998; Li 1998; Ning et al. 2000; Tsai et al. 2005, 2008).

Temperature, nitrate availability and light conditions are factors generally accepted to control long-term variation in *Synechococcus* distribution (Lantoine and Neveux 1997), although grazing and advection can regulate short-term population changes. Andersson et al. (1994) found that temperature influenced the development of picophytoplankton more strongly than it affected micro- and nano-phytoplankton. Agawin et al. (1998) found a close positive relationship between temperature and *Synechococcus* growth rates (0 to 2.3 d^{-1}) across a wide temperature range (-0.5 to 25°C) in a bay of the Mediterranean Sea. In temperate waters, the annual cycle of *Synechococcus* abundance is quite regular. Generally, *Synechococcus* is most abundant in summer and least so in winter (Kuosa 1991; Agawin et al. 1998; Ning et al. 2000). Likewise, in a boreal inshore area where surface temperatures ranged from 0.7 to 21.6°C, a large seasonal variation in *Synechococcus* abundance (1.3 to 19 × 10^4 cells mL^{-1}) was noted (Jochem 1988). However, warm tropical seas have less temperature variation than temperate seas. For example, at Station ALOHA in Hawaiian waters, the annual average temperature was 24.9°C and low *Synechococcus*

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abundance (annual average about 1.4 × 103 cells mL^{-1}) was observed (Campbell et al. 1997). On a global scale, Li et al. (1998) found that the average annual abundance of *Synechococcus* was correlated to the average annual temperature below 14°C, but not above 14°C. This result suggests that factors other than temperature, such as nutrient limitation or predation, have greater influence on *Synechococcus* abundance in warmer tropical seas that have less temperature variation. In this note, we examine the hypothesis that temperature, in particular its relative variability, is a major physical factor predicting seasonal variations of *Synechococcus* abundance across a wide geographic range.

2. MATERIAL AND METHODS

2.1 Study Site, Sample Collection and Enumeration

The East China Sea (ECS) is located on the western edge of the northwest Pacific Ocean and is characterized by dynamic interactions among water systems including nutrient enriched flow from the Changjiang River (Gong et al. 1996). In addition to freshwater input from the Changjiang River, three other water masses influence the ECS: the Yellow Sea Coastal Water (YSCW) from north to south along the northwest coast of the sea, the Kuroshio Water (KW), and the Taiwan Current Warm Water (TCWW). The KW system is located adjacent to the outer deep-water region of the ECS and is distinguished by its high temperature and high salinity (Miao and Yu 1991); the TCWW is composed of waters originating from northward flow through the Taiwan Strait and shelf-intrusion waters of the Kuroshio Current (Jan et al. 2002, 2010).

Samples for *Synechococcus* abundance, temperature and salinity were collected by CTD from 29 stations across a wide area of the ECS in December 1997 and March, June, July, October and November 1998 (numbered stations, Fig. 1). Additional samples were collected monthly by CTD casts at six fixed stations (A through F, Fig. 1) in the southern East China Sea (ECS) during 2004, except for February, March, October and December. During all cruises, samples to determine *Synechococcus* abundance were fixed immediately with glutaraldehyde (final concentration 1%, v/v). For *Synechococcus* enumeration, 4 - 10 mL of seawater were collected using low pressure on a 0.2 µm pore size Nuclepore filter and examined without staining at 1000× magnification with a Nikon Optiphot-2 epifluorescence microscope. *Synechococcus* were identified by their orange autofluorescence under the blue excitation light. At least 400 *Synechococcus* were counted per sample.

To compare effects of temperature on abundance, we defined an index of the seasonal abundance cycles of *Synechococcus* ($\Delta N/N_{min}$), where ΔN is the difference between the minimum and maximum *Synechococcus* abundance

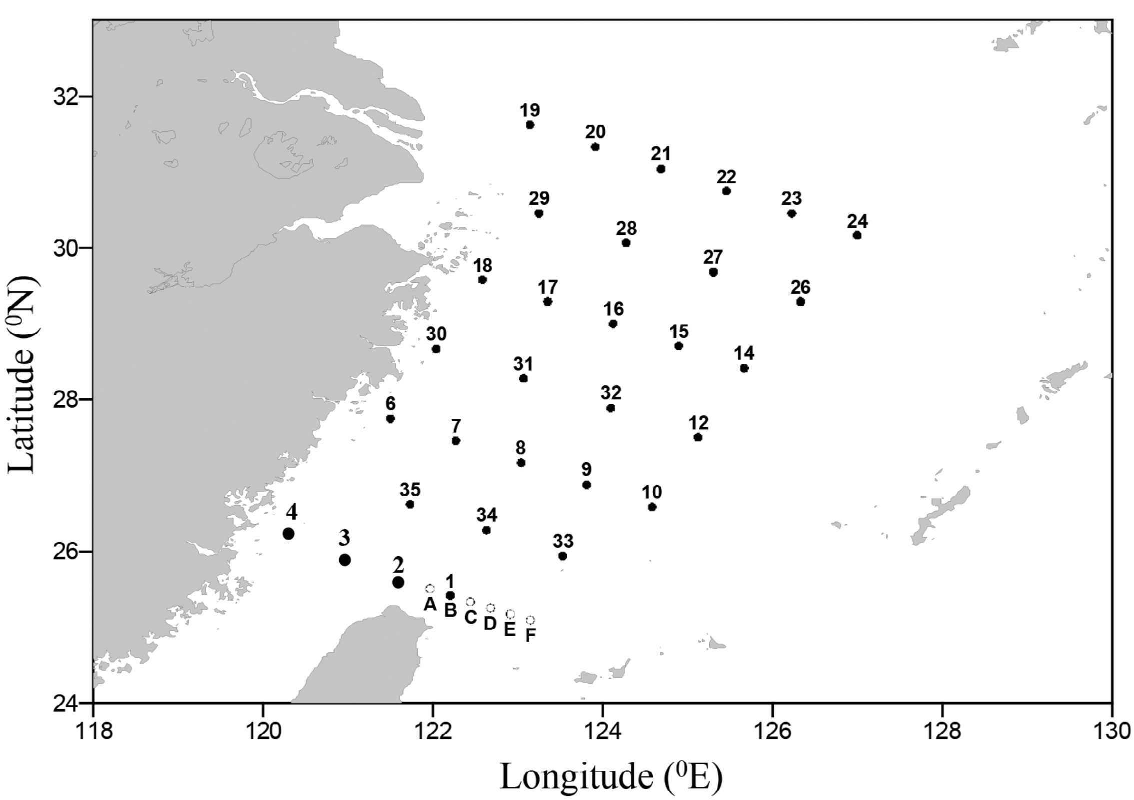

Fig. 1. Sampling sites in the East China Sea (ECS) for a series of monthly cruises in 2004 (Stations A - F) (○) and for thirty sites sampled during four cruises in 1997-1998 (Stations 1 - 35) (●).

over a seasonal cycle, and N_{min} is the minimum *Synechococcus* density during that time period. The range of sea surface temperature (ΔT) was the difference between the annual minimum and maximum temperatures. The coefficients of variation (CV) of *Synechococcus* density and of temperature also were determined to quantify their seasonal variation. These data from the ECS were compared with literature values of *Synechococcus* abundance and temperature collected in temperate and tropical oceans (Table 1).

3. RESULTS AND DISCUSSION

The index of seasonal change in *Synechococcus* abundance ($\Delta N/N_{min}$) for the ECS in 2004 ranged from 7.6 (Station F) to 18.4 (Station C) and the seasonal difference of temperature (ΔT) ranged from 6.1 at Station E to 10.7 at Station A (Table 2). The index increased with increasing ΔT for these stations (Fig. 2a). Data from the four cruises in the ECS during 1997/1998 included a wider range of ΔT (Table 2, Fig. 1), but reflected the trend observed in 2004. A significant positive relationship ($p < 0.05$) was found between $\Delta N/N_{min}$ and the annual temperature range, ΔT (Fig. 3a) for the ECS, indicating a strong effect of the seasonal range of surface water temperature on *Synechococcus* abundance. The correlation between the CV of *Synechococcus* density and the CV of temperature was also statistically significant ($p < 0.05$) (Figs. 2b and 3b), suggesting that less variable thermal environments resulted in a reduced seasonal range of *Synechococcus* abundance. Furthermore, a significant negative relationship ($p < 0.05$) was found between $\Delta N/N_{min}$ and annual average temperature, mean T (Fig. 3c) for the ECS; this result suggests that factors other than temperature, such as nutrient limitation or predation (Li et al. 1998), have greater influence on *Synechococcus* abundance in warmer tropical

Table 1. Locations and seasonal ranges of temperature and *Synechococcus* abundance from previous.

Location	Station	Temperature (°C)		*Synechococcus* (cells mL^{-1})		Reference
		Min	Max	Min	Max	
Newfoundland, Canada	Conception Bay	-2	14	700	19000	Putland (2000)
Florida, USA	Pensacola Bay (subtropical estuary)	10	31	8000	3000000	Murrell and Lores (2004)
Northern Baltic Sea	Tvärminne	0.7	23.3	7000	750000	Kuosa (1991)
Eastern Africa	Lake Kivu	23.1	24.2	74000	142000	Sarmento et al. (2008)
Eastern Mediterranean	Northern Levantine Basin	15.2	30.48	6418	153562	Uysal and Köksalan (2006)
NW Mediterranean Sea	Blanes Bay	11	26	500	60000	Agawin et al. (1998)
Taiwan	Subtropical Western Pacific Coastal site	17	29	2000	110000	Chang et al. (1996)
Australia	Davies Reef Lagoon	22.8	28.4	12000	100000	Ayukai (1992)
San Francisco Bay USA	North Bay	13.4	22.3	55000	199000	Ning et al. (2000)
San Francisco Bay USA	Central Bay	13.2	18.2	16000	54000	Ning et al. (2000)
San Francisco Bay USA	South Bay	13.5	21.7	44000	234000	Ning et al. (2000)
NW Mediterranean	Coastal Lagoon	6.5	23.5	250	8200	Bec et al. (2005)
Southern Taiwan	Lagoon	23.9	31.5	400	1300	Tsai et al. (2009)
Japan	Suruga Bay	15	25	4000	35000	Shimada et al. (1995)
Mediterranean Eutrophic Area	Bay of Naples	14	27.8	1600	69300	Modigh et al. (1996)
Italy	Valley	22	29	2000	16000	Andreoli et al. (1989)
Italy	Lagoon	7	30	2000	10000	Andreoli et al. (1989)
Adriatic Sea	Coastal Water	11.4	26.5	1900	62000	Gladan et al. (2006)
USA	Chesapeake Bay	6	27	260	81000	Wang and Chen (2004)

Table 2. The seasonal ranges of temperature and *Synechococcus* abundance, seasonal average temperature (mean T) and difference (ΔT), index of *Synechococcus* abundance change ($\Delta N/N_{min}$), and the coefficients of variation (CV) for temperature and *Synechococcus* abundance in the ECS during 2004 (Stations A - F) and 1997 - 1998 cruises (Stations 1 - 29).

Stations	T (°C)	*Synechococcus* (104 cells mL^{-1})	mean T	ΔT	$\Delta N/N_{min}$	T (CV)	*Synechococcus* (CV)
A	18.7 - 29.4	0.6 - 9.2	24.8	10.7	13.80	17	71
B	19.7 - 29.9	0.5 - 7.0	24.7	10.2	16.55	14	65
C	20.1 - 30.0	0.3 - 5.4	25.7	9.8	18.39	15	90
D	21.1 - 30.0	0.3 - 3.1	27.1	8.9	9.13	11	75
E	24.4 - 30.5	0.4 - 1.2	27.8	6.1	8.23	8	46
F	24.3 - 30.6	0.1 - 1.2	27.7	6.3	7.57	8	58
1	20.9 - 28.5	1.9 - 11.4	25.0	7.6	7.03	13	85
2	19.3 - 28.8	0.7 - 11.2	23.4	9.5	14.56	18	111
3	16.5 - 28.5	0.3 - 12.3	22.1	12.0	48.36	25	150
4	13.1 - 26.0	0.2 - 5.9	19.1	12.9	30.16	30	157
6	12.0 - 26.0	0.2 - 16.3	18.7	14.0	84.79	35	180
7	20.0 - 27.9	1.4 - 2.4	23.2	7.9	3.11	16	73
8	19.8 - 27.4	1.9 - 8.6	23.0	7.6	3.56	15	75
9	21.4 - 27.6	1.7 - 4.3	23.9	6.2	1.44	12	50
10	21.3 - 29.3	0.7 - 1.9	25.7	8.0	1.85	15	51
12	18.6 - 28.8	0.8 - 8.4	24.4	10.2	9.58	18	80
14	15.9 - 27.2	0.3 - 7.8	22.8	11.3	30.04	21	122
15	14.3 - 26.6	0.4 - 7.9	21.4	12.3	19.21	25	135
16	13.6 - 26.7	0.3 - 9.4	20.9	13.1	36.72	27	103
17	12.3 - 25.8	0.3 - 5.1	20.0	13.5	18.58	30	101
18	11.7 - 22.8	0.4 - 4.9	17.4	11.1	11.25	34	77
19	11.1 - 22.0	0.3 - 3.0	16.9	10.9	9.00	31	78
20	11.2 - 25.0	0.2 - 1.5	18.5	13.8	6.50	34	87
21	11.7 - 22.6	0.2 - 8.4	18.0	10.9	42.95	28	138
22	12.5 - 25.2	0.3 - 12.6	19.4	12.7	34.00	30	161
23	14.1 - 25.3	0.5 - 17.3	20.5	11.2	36.61	25	106
24	17.1 - 26.8	0.5 - 4.9	22.6	9.7	7.91	19	86
26	16.6 - 27.1	0.5 - 14.5	22.7	10.5	29.85	20	130
27	15.5 - 27.5	0.5 - 8.1	21.5	12.0	14.88	24	93
28	14.3 - 26.8	0.3 - 7.1	20.8	12.5	22.77	26	121
29	13.6 - 24.5	0.4 - 4.2	19.7	10.9	9.50	26	76

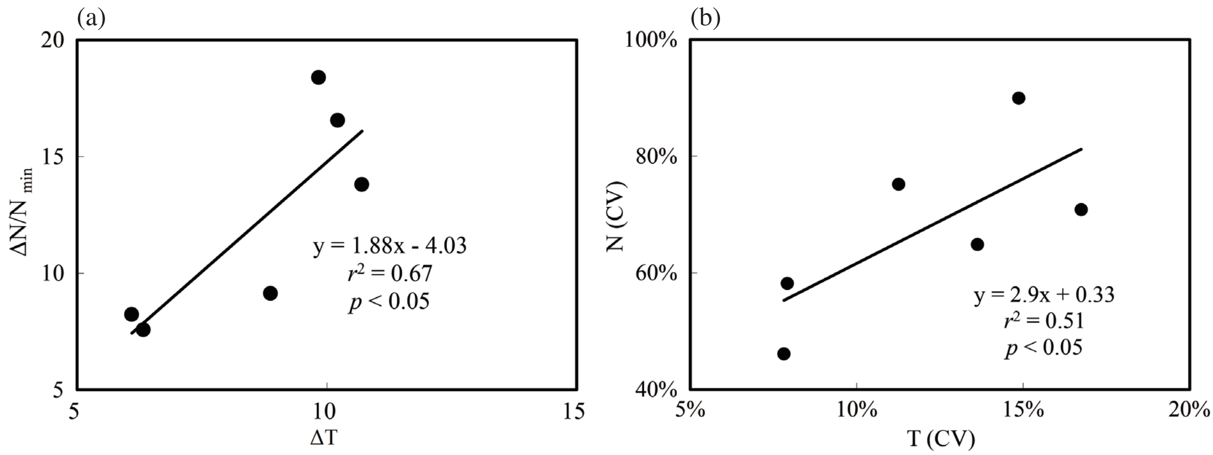

Fig. 2. (a) Index of *Synechococcus* abundance ($\Delta N/N_{min}$) versus ΔT, the reported range of annual temperature, and (b) CV of *Synechococcus* abundance vs. CV of temperature for six sampling sites in the southern ECS during 2004.

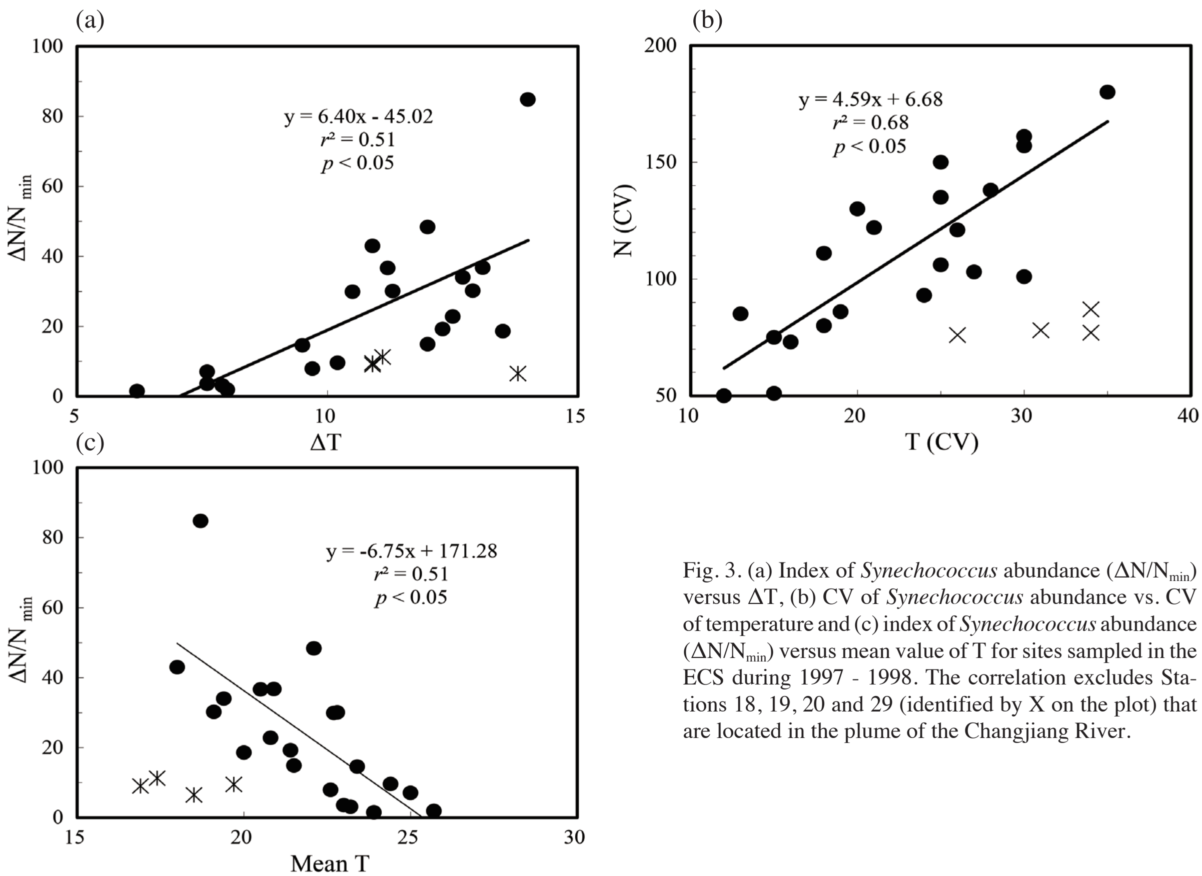

Fig. 3. (a) Index of *Synechococcus* abundance ($\Delta N/N_{min}$) versus ΔT, (b) CV of *Synechococcus* abundance vs. CV of temperature and (c) index of *Synechococcus* abundance ($\Delta N/N_{min}$) versus mean value of T for sites sampled in the ECS during 1997 - 1998. The correlation excludes Stations 18, 19, 20 and 29 (identified by X on the plot) that are located in the plume of the Changjiang River.

seas that have less temperature variation. A similar relationship ($p < 0.05$) between ΔT and $\Delta N/N_{min}$ was demonstrated for data from the literature, including information from both tropical and cold temperate oceans (Table 1, Fig. 4).

For some stations, the large seasonal range in temperature was not reflected by high seasonal variations of *Synechococcus* abundance. Some data from the 1997/1998 ECS cruises and from the literature indicated high ΔT associated with low $\Delta N/N_{min}$, and were excluded from the analyses (Fig. 3b). The excluded samples were collected from turbid coastal or estuarine waters including the Changjiang River plume of the ECS (Fig. 3b, Stations 18, 19, 20 and 29). The limited growth of *Synechococcus* in some coastal areas has been attributed to increased turbidity from land-derived suspended sediment during summer with resultant light limitation of picophytoplankton growth (Vaulot and Ning

1988; Chiang et al. 2002; Pan et al. 2007). However, summer chl *a* concentrations exceeded 10 μg L^{-1} near the Changjiang River plume (Gong et al. 1996), and were > 20 μg L^{-1} in Pensacola Bay (Murrell and Lores 2004). This suggests that light did not limit primary production at these sites. Similar results in the St. Lawrence River transition zone indicated that the phytoplankton were well adapted to the intermittent exposure to bright light that occurred in the turbid, well-mixed waters (Vincent et al. 1994). Other possible factors limiting *Synechococcus* abundance in these areas include competition for nutrients with larger phytoplankton (Chisholm 1992; Ning et al. 2000), and grazing pressure that can be higher on picophytoplankton than on larger cells (Lovejoy et al. 1993; Vincent et al. 1994; Calbet 2001; Winkler et al. 2003).

As noted previously, variations in *Synechococcus* distributions are likely to be the result of interactive effects of temperature, nutrient and light conditions, and possible grazing (e.g., Lantoine and Neveux 1997). Li et al. (1998) indicated that nutrient limitation could be a major factor affecting *Synechococcus* abundance at higher temperatures. Chang et al. (2003) also suggested that nutrients might become more important in controlling the spatial distribution of *Synechococcus* growth in regions with water temperature higher than 16°C. This is consistent with our analyses because low ΔT and generally higher temperatures are found in tropical areas where nutrient limitation could result in a reduced abundance index ($\Delta N/N_{min}$) for *Synechococcus*. In temperate areas there is a larger annual range of temperatures and *Synechococcus* densities at cold temperatures are much lower than the minimum abundances observed in the tropics. These regional differences are reflected by $\Delta N/N_{min}$, which is driven strongly by N_{min}. While N_{max} does not correlate significantly with ΔT (Figs. 5a, c), *Synechococcus* minimum abundance was inversely related to ΔT for both ECS and other areas (Figs. 5b, d; $p < 0.05$). This suggests that seasonal cold temperatures result in seasonally

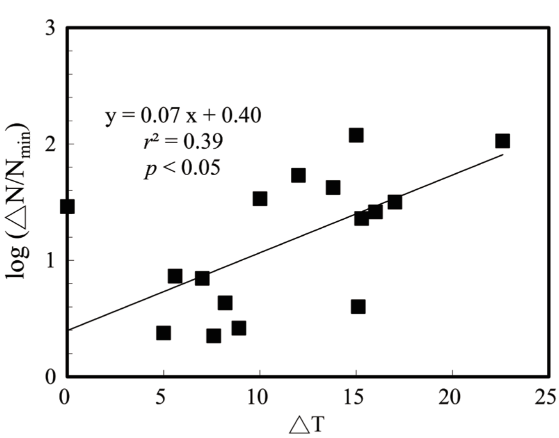

Fig. 4. Index of *Synechococcus* abundance ($\Delta N/N_{min}$) versus ΔT for literature data from Table 1.

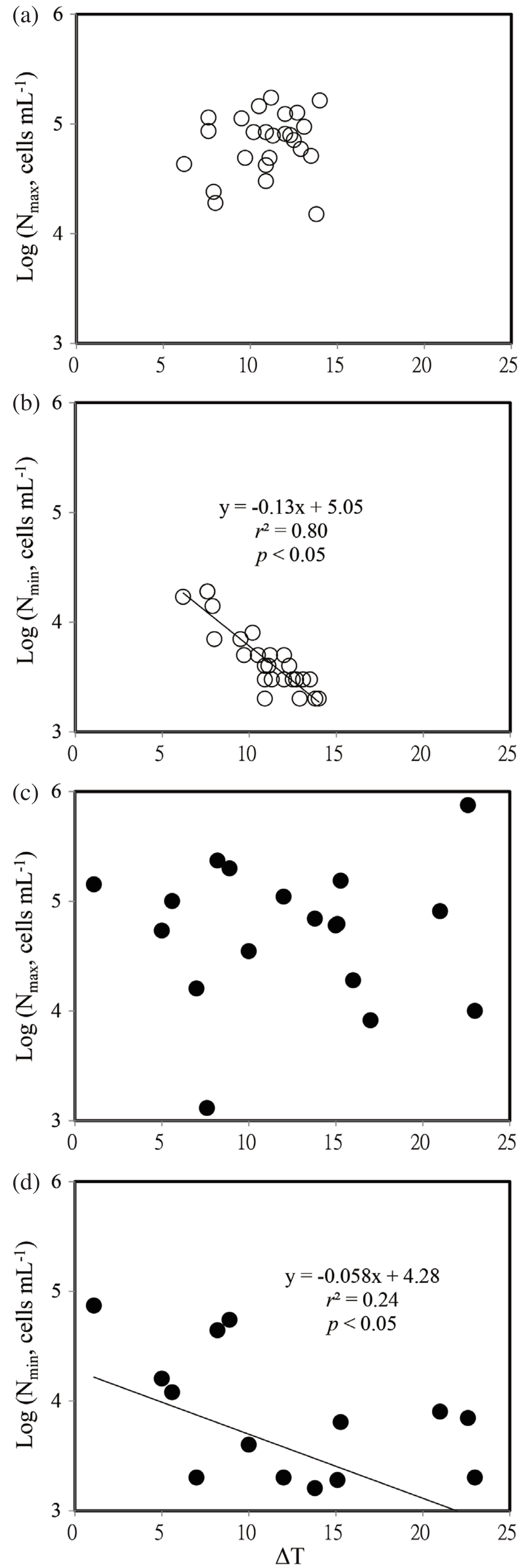

Fig. 5. *Synechococcus* maximum (N_{max}) and minimum (N_{min}) abundance related to ΔT in the ECS (A, B) (○) and from literature reports (C, D) (●).

very low *Synechococcus* abundance in temperate areas, although the relationship holds in the subtropical ECS, which is influenced by water masses with widely different temperatures (Fig. 5b). Grazing effects by irregular population peaks in heterotrophic protists also could result in reduced picoplankton abundance in temperate waters.

In conclusion, the range of temperature (ΔT) in a given environment is a relatively good predictor for seasonal change in *Synechococcus* abundance across many open ocean environments. While many factors affect population size in picoplankton, our current assessment of the variability of temperature and *Synechococcus* abundance suggests that tropical oceans, unlike temperate oceans, are characterized by lower amplitude fluctuations in *Synechococcus* abundance attributable in part to lower seasonal variations of temperature.

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