REVIEW PAPER

Effect of temperature change on physiology and biochemistry of algae: A review

Ming-Li Teoh[1*], Wan-Loy Chu[2] & Siew-Moi Phang[3]

[13]Institute of Graduate Studies & Institute of Ocean & Earth Sciences, University of Malaya, 50603 Kuala Lumpur, Malaysia;
[2]International Medical University, No. 126, Jalan 19/155B, Bukit Jalil, 57000 Kuala Lumpur, Malaysia;
* teoh@um.edu.my (Corresponding author); phone: +603-79674640; fax: +603-79676994;
Received on 11th March 2010, accepted by 15th July 2010

ABSTRACT The productivity and survival of algae are strongly affected by their physiological and biochemical processes, as well as biotic and abiotic factors in the environment. In recent years, global climate change such as increased temperature and elevated ultraviolet radiation (UVR) due to ozone depletion has huge impact on organisms particularly the ones in the marine ecosystem. It has been demonstrated that the global temperature increased steadily over the last decade, with an average of 0.74°C. In the coming years, climate model projections summarized by the Intergovernmental Panel of Climate Change (IPCC) indicate that average global surface temperature will likely rise a further 0.5 to 1.6°C by 2030, and rising to 1.1 to 6.4°C by 2100. As algae serve as the primary producer of food chain in both marine and terrestrial ecosystems, it is of great significance to understand the impact of temperature change on their physiological and biochemical processes. This review provides the information on how algae respond to temperature change based on their growth, biochemical composition and fatty acid composition.

ABSTRAK Produktiviti dan kelangsungan hidup alga sangat dipengaruhi oleh proses fisiologi dan biokimia mereka, serta faktor-faktor biotik dan abiotik dalam persekitarannya. Dalam beberapa tahun terakhir, perubahan iklim global seperti kenaikan suhu dan peningkatan radiasi ultra-ungu (UVR) akibat penipisan lapisan ozon mempunyai kesan besar terhadap organisma khususnya yang berada dalam ekosistem marin. Telah terbukti bahawa suhu global meningkat secara berterusan sejak berdekad-dekad terakhir, dengan purata 0.74°C. Dalam tahun-tahun akan datang, unjuran-unjuran model iklim yang diringkaskan oleh Intergovernmental Panel of Climate Change (IPCC) menunjukkan bahawa purata suhu permukaan global berkemungkinan akan meningkat menjadi 0.5 hingga 1.6°C pada tahun 2030, dan meningkat menjadi 1.1 hingga 6.4°C pada tahun 2100. Memandangkan alga berperanan sebagai pengeluar utama rantai makanan di kedua-dua ekosistem marin dan darat, adalah sangat penting untuk memahami kesan perubahan suhu terhadap proses fisiologi dan biokimia mereka. Ulasan ini menyediakan maklumat tentang bagaimana alga bertindak balas terhadap perubahan suhu berdasarkan pertumbuhan, komposisi biokimia dan komposisi asid lemak mereka.

(**Keywords**: Global warming, algae, temperature, biochemical composition, fatty acid)

INTRODUCTION

During the last few decades, changes in global environment such as global warming and ozone depletion have been particularly strong and are topics of great concern. Global climate change is making itself felt in the form of prolonged droughts, warmer air and ocean temperature, increase land-surface precipitation, melting glaciers and ice caps, rising in sea level, thawing of permafrost and changes in atmosphere and oceanic circulation patterns (IPCC, 2007). The effects of climate change such as global warming and increased UVR on algae have been receiving increase interest (Teoh et al., 2004; Chu et al., 2005; Wong et al., 2007). There is strong evidence which shows that the average global temperature will increase with the increase of anthropogenic greenhouse gasses such as carbon dioxide (CO_2), nitrous oxide (N_2O), ozone (O_3), methane (CH_4) and chlorofluorocarbons (CFCs) in the atmosphere.

The elevated anthropogenic greenhouse gases would lead to an increase in the average global

surface temperatures ranging anywhere from 1.8 to 4.0°C, though the actual rise will not be homogenous and some parts of the world will see far larger shifts in temperature than this (Kojima & Harrison, 1998; Hostetler & Small, 1999; IPCC, 2007).
To date, only few authors reported about the issues of global warming in Malaysia (Quadir et al., 2004; Ng et al., 2005; Tangang et al., 2007). Ng et al. (2005) observed a significant increase of the mean annual temperature ranging from 0.99 to 3.44°C / 100 years for the period of 50 years (1951 – 2001) in Malaysia. In a similar study, the surface temperatures in most regions in Malaysia showed significant warming trends of between 2.7 to 4.0°C / 100 years during the last 42 years from 1961 to 2002 (Tangang et al., 2007).

Global warming can have a huge impact on all organisms on Earth. The impact on algae can be far reaching as they are important biotic component in the world's ocean and freshwater ecosystems and account for around 50 % of the net amount of 111 – 117 Pg C assimilated annually (1 Pg = 10^{15} g) by photoautotrophs (Behrenfeld et al., 2001; Beardall & Raven, 2004; Falkowski & Raven, 2007). This will eventually affect the whole ecosystem where changes in the food chain will cause changes in the species composition and abundance of organisms up the food chain.

One of the main topics that captured the attention of scientists around the world is the concern on how environments are changing, and how these changes are affecting, or going to affect life on Earth and how it might respond (Peck, 2005; Beardall & Stojkovic, 2006; Beardall et al., 2009). According to Peck (2005), organisms have a limited number of responses that enhance survival in changing environments. These are:

1. To cope with the change using internal physiological flexibility and capacities,
2. To evolve adaptations to the new conditions, or
3. To migrate to areas consistent with survival.

If the organisms failed to migrate or adapt to the changing environment, they will become extinct. With increased temperature, this phenomenon will lead to accelerated growth rate and metabolic activity of algae which is generally positively correlated with temperature within a suitable range. Therefore, temperature is an important factor controlling growth rate, physiological and metabolic processes in algae (Beardall & Raven, 2004; Chu et al., 2005; Staehr & Birkeland, 2006). In addition, there have been several studies on temperature as an important determinant of species composition and geographical distribution of algae (Bischoff & Wiencke, 1995; Pakker et al., 1995; Butterwick et al., 2005).

Response of algae to increased temperature

Growth Rate

Temperature is a fundamental environmental factor that strongly regulates the algal growth (Eppley, 1972; Raven & Geider, 1988). The relationship between temperature and a given biological rate such as algal growth and photosynthesis has often been described by the temperature coefficient Q_{10} or Arrhenius functions (the factor by which a biological rate is increased by a 10ºC rise in the temperature) (Ahlgren, 1987; Regier et al., 1990). The use of Q_{10} values assumes an Arrhenius–type relationship between growth rates and temperature. Conversely, both of these functions assume continuous acceleration of growth with increasing temperature. It is assumed that the algal growth rates increase up to the optimal temperature (T_{opt}), beyond which they decrease (Suzuki & Takahashi, 1995; Montagnes & Franklin, 2001).

Temperature is a very important ecological parameter that affects almost every aspect of aquatic life. The effects may vary from increase in the metabolic rate of organisms to displacement or even mortility of sensitive organisms (Rajadurai et al., 2005). The temperature-growth range of an alga is important ecologically because it defines the range over which the alga can be metabolically active and determines the distribution of algae. Different algal species have different ranges of tolerance and physiological responses to temperature changes (Table 1). According to Li (1980), some algae can survive at extreme habitats with temperatures ranging from – 2°C in the Arctic and Antarctic to 75°C in thermophilic hot springs.

A study on the temperature-growth characteristics of 35 taxa (128 isolates) from Antarctic oases showed that all isolates grew at temperatures ranging from 7.5 to 18°C with about 6% of the 128 clones unable to grow at ≤ 5°C. Nevertheless, over one-third of the isolates can tolerate high temperature of 30°C (Seaburg et al., 1981). For example, Suzuki & Takahashi (1995) studied the growth responses of several diatoms exposed to different culture temperatures and found that these diatoms showed a maximum growth rate at the temperature very near to the upper limit, which was generally higher than the isolation temperature. In a study on six Antarctic algae showed that they grow above ambient temperature (Teoh et al., 2004).

Although it is generally assumed that cyanobacteria have high temperature optima for growth (> 20°C), cyanobacteria are often the dominant autotrophic

Table 1: Temperature tolerance and temperature optima of microalgae isolated from different habitats.

Species	Origin	Temperature optima (°C)	Temperature tolerance (°C)	μ optima (d^{-1})	Reference
Chlainomonas kolii	Washington	0 – 4	0 – 4	-	Hoham (1975)
Chlainomonas rubra	snow	0 – 4	0 – 4	-	
Chloromonas pichinchae		1	0 – 10	-	
Cylindrocystis brebissonii		10	0 – 20	-	
Raphidonema nivale		5	0 – 15	-	
Clamydomonas globosa	Antarctic	18 – 20	5 – 20	1.76 – 1.82	Seaburg et al.
Chlamydomonas intermedia	oases	15 – 18	-1 – 18	1.54 – 1.58	(1981)
Chlamydomonas		10 – 12.5	-1 – 18	1.10 – 1.35	
subcaudata		12.5 – 15	-1 – 18	1.04 – 1.42	
Chloromonas alpine					
Nitzschia seriata	Arctic	6 – 12	-1.6 – 12	0.361 – 0.567	Smith et al. (1994)
Mastigocladus laminosus	Hot spring	26 - 50	45	0.023	Singh et al. (1994)
Laurencia sp.	Tropical	25 – 30	15 – 30	-	Bischoff-
Laurencia cartilaginea	island	30	15 – 30	-	Basmann et al.
Hypnea cenomyce	Hainan,	30	15 – 30	-	(1997)
Hypnea spinella	Peoples Republic of China	30	15 – 30	-	
Cyanobacteria (27 isolates)	Arctic Subarctic Antarctica	15 – 35	5 – 35	0.12 – 0.41	Tang et al. (1997a)

*μ optima: Specific growth rate (s) at optimal temperature(s)

Table 2: Temperature tolerance and temperature optima of microalgae isolated from different habitats (continue).

Species	Origin	Temperature optima (°C)	Temperature tolerance (°C)	μ optima (d^{-1})	Reference
Cyanobacterial assemblages	Antarctica	20	0 – 45	-	Fritsen & Priscu (1998)
Phormidium subfuscum	Antarctica	15	5 – 20	0.26	Tang & Vincent (1999)
Phormidium tenue	Arctic	30	10 – 40	0.84	
Oscillatoria spp. (2 isolates)	Antarctic meltwater ponds	8	3 – 18	0.08 – 0.12	Nadeau & Castenholz (2000)
Nannochloropsis oceanica	Temperate	25 – 29	14.5 – 35.7	1.6	Sandnes et al. (2005)
Chaetoceros wighami	Tropical	28	28 – 40	-	Rajadurai et al. (2005)
Amphora coffeaeformis		28 – 33	28 – 40	-	
Micromonas sp.	Arctic	6 – 8	0 – 15	0.55	Lovejoy et al. (2007)
Chlamydomonas sp. ARC	Chukchi sea ice, Alaska	5	-10 – 20	0.41	Eddie et al. (2008)
Amphidinium sp.	Okinawa, Japan	24 – 29	21 – 35	0.022 h^{-1}	Kitaya et al. (2008)
Chlorella sp. R-06/2	Rupite, Bulgaria	26 – 39	15 – 51	-	Gacheva & Pilarski (2008)

*μ optima: Specific growth rate (s) at optimal temperature(s)

Table 3: Temperature tolerance and temperature optima of microalgae isolated from different habitats (continue).

Species	Origin	Temperature optima (°C)	Temperature tolerance (°C)	μ optima (d^{-1})	Reference
Chlorella sp., strain BI	Transitory pond near Bratina Island, Antarctica	10	4 - 20	0.33 – 0.44	Morgan-Kiss et al. (2008)
Chloromonas chenangoensis	Chenango Valley, NY Whiteface Mnt., NY	2.5 – 5.0	0 – 7.5	-	Hoham et al. (2008)
Chloromonas rosae v. *psychrophila*	White Mnt., AZ Tughill Plateau, NY	4 – 15	0 – 20	-	
Chloromonas rosae v. *psychrophila*		4 – 15	0 – 20	-	
Chloromonas tughillensis		2.5 – 5.0	0 – 10	-	
Symbiodinium californium	Santa Barbara, California	15 – 28	5 – 30	0.21 – 0.26	McBride et al. (2009)

*μ optima: Specific growth rate (s) at optimal temperature(s)

Table 4: Biochemical composition variation to temperature stress.

Species	Origin	Temperature	Effect	Reference
Chaetoceros calcitrans, Thalassiosira pseudonana, Chaetoceros simplex, Chaetoceros gracilis, Phaeodactylum, Dunaliella tertiolecta, Pavlova lutheri, Isochrysis galbana	Temperate	10, 15, 20 and 25°C	Protein per cell had minimum values at intermediate temperatures; lipid and carbohydrate per cell showed no consistent trends with temperature	Thompson et al. (1992a)
Isochrysis galbana TK1	Temperate (Taiwan)	15 and 30°C	15°C → highest protein and carbohydrate content 30°C → higher lipid content	Zhu et al. (1997)
Spirulina maxima *Spirulina platensis*	Tropical	20, 25, 30,35 and 40°C	↑ temperature →↓ protein content; ↑ carbohydrate content	Oliveira et al., (1999)
Chaetoceros sp. (CS256) *Rhodomonas* sp. (NT15) *Cryptomonas* sp. (CRFI01) Prymnesiophyte (NT19) *Isochrysis* sp. (clone T.ISO)	Tropical	25, 27, 30, 33 and 35°C	> 27°C → significantly lower % protein content; no consistent trend in the % carbohydrate content	Renaud et al. (2002)
Thalassiosira pseudonana	Temperate	8, 17 and 25°C	Protein content remain constant across different temperatures	Berges et al. (2002)

Table 5: Biochemical composition variation to temperature stress (continued).

Species	Origin	Temperature	Effect	Reference
Caulerpa spp. (six *Caulerpa* species)	Temperate (Gulf of Mexico)	Rainy season (30.2°C) Cold season (25.7°C) Dry season (27.6 – 30.3°C)	Dry season: ↑ seawater temperature, ↑ protein content Rainy and cold seasons: ↓ seawater temperature, ↑ carbohydrate content	Robledo & Freile-Pelegrin (2005)
Chaetoceros cf. *wighamii*	Southern Atlantic Ocean waters, Brazil	20, 25 and 30°C	20 and 25°C → higher lipid and carbohydrate content; protein was unaffected	de Castro Araujo & Garcia (2005)
Nannochloropsis sp.	Qingdao, China	14, 22 and 30°C	High and low temperature (14 and 30°C) → ↑ lipids and protein contents	Hu & Gao (2006)
Chlorella vulgaris		25, 30, 35 and 38°C	25 to 30°C→ ↓ lipid from 14.71 to 5.90%	Converti et al. (2009)
Nannochloropsis oculata		15, 20 and 25°C	20 to 25°C→ ↑ lipid from 7.90 to 13.89%	

Table 6: Effect of temperature on fatty acid composition of selected microalgae reported in the literature.

Microalgae	Origin	Temperature change	Effect	Reference
Spirulina platensis UTEX 1928	Temperate	25 – 38°C	↑ temperature : total fatty acid ↓ from 37% to 19% % 18:3 ↓ Ratio of unsaturated fatty acid: saturated fatty acid ↓ with increasing temperature	Tedesco & Duerr (1989)
Anksitrodesmus convolutes UMACC 101	Tropical	18, 28 and 38°C	↑ temperature : 18:3 ↓ 16:0 and 18:1 ↑	Chu et al. (1994)
Chlorella vulgaris strain SO-26	Antarctica	10 – 20°C	↓ temperature : % 16:0 ↓ % 18:3 ↑ Ratio of unsaturated fatty acid: total fatty acid ↑ from 53.7 to 64.0%.	Nagashima et al. (1995)
Chaetoceros sp. *Rhodomonas* sp. *Cryptomonas* sp. Unidentified prymnesiophyte *Isochrysis* sp.	Tropical	25 – 35°C	Higher growth temperature: % 20:5 and % 22:6 ↓	Renaud et al. (2002)

Table 7: Effect of temperature on fatty acid composition of selected microalgae reported in the literature (continued).

Microalgae	Origin	Temperature change	Effect	Reference
Spirulina platensis *Chlorella vulgaris* *Botryococcus braunii*	Temperate	30 – 40°C 20 – 30°C 18 – 32°C	*Spirulina platensis*: At 30 ^{o}C, 16:0 was higher At 40 ^{o}C, 16:1, 18:2ω6 and 18:1ω3 was lower	Sushchik et al. (2003)
Navicula UMACC 231	Antarctic	4 – 30°C	↑ temperature: PUFA ↓	Teoh et al. (2004)
Pheodactylum tricornutum	Temperate	10 – 25°C	↓ temperature : Yields of PUFA and EPA ↑ by 120% % EPA ↑ by 85% % 16:0 ↓ by 30% % 16:1 ↓ by 20%	Jiang & Gao (2004)
35 *Arthrospira* strains	Temperate	20 – 30°C	↓ temperature: % 18:2 and 18:3 ↑ % 16:0 ↓	Muhling et al. (2005)
Nannochloropsis sp.	Temperate	14 – 30°C	↑ temperature: % 16:0 ↑ % 20:5 ↓	Hu & Gao (2006)
Spirulina platensis C1	Tropical	35 – 43°C	↑ temperature: % 18:2 ↑ % 18:3 ↓	Chaiklahan et al. (2007)

community which form mats and films across the benthic substrate in many types of lakes, streams, and ponds in the Arctic and Antarctica (Tang et al., 1997a, b; Fritsen & Priscu, 1998; Nadeau & Castenholz, 2000; Chevalier et al., 2000; Sutherland, 2009).

A study on 27 isolates of high-latitude mat-forming cyanobacteria from the polar (Arctic, sub-Arctic and Antarctic) freshwater ecosystems, Tang et al. (1997a) found that the temperature optimum for growth ranged from 15 – 35°C, with an average of 19.9°C. The study showed that maximal growth rates of the algae occurred within the upper limit for growth and generally higher than the ambient temperature from which the species were isolated. Similar findings were observed for the cyanobacterial assemblages from several permanent ice covers in Antarctica, where optimum rates of photosynthesis occurred at temperatures > 15°C (Fritsen & Priscu, 1998).

Temperate can impose a significant effect on the specific growth rate of algae. At temperature below optimum for growth, µ increases with increasing temperature but declines markedly at above the optimal temperature. For example, the growth rates of three tropical Australian algae *Cryptomonas* sp., *Rhodomonas* sp. and prymnesiophyte NT19 increase with temperature within 25 to 30°C, but decline at temperatures above 30°C (Renaud et al., 2002).

Similarly, *Nannochloropsis oceanica* showed increasing µ as a function of temperature, from 14.5°C, with a peak at 25 – 29°C. Above 30°C the cultures showed dramatic reduction in µ, with no cultures growing at temperatures over 35°C (Sandnes et al., 2005). In the marine diatom *Chaetoceros calcitrans*, the growth rates increased with temperature from 0.3 d^{-1} at 6°C to 1.0 d^{-1} at 15°C, and 1.4 d^{-1} at 25°C (Anning et al., 2001). Similar trends were observed in two mesophilic microalgae, *Microcystis aeruginosa* and *Scenedesmus acutus* (Staehr & Birkeland, 2006), an Arctic cyanobacterium, *Schizothrix calcicola* (Tang & Vincent, 2000) and *Phormidium sp.* from a high Arctic lake (Tang et al., 1997b) where µ increased with increasing temperature from 5 to 25°C.

Biochemical Composition

There have been intensive studies on the biochemical composition of algae as they are the primary producers in the food chain. Information on the nutritional properties of algae such as protein, carbohydrate and lipid content is crucial and could be a useful prediction to account for the efficiency of biomass transfer between the trophic levels (Thompson et al., 1992a; Gatenby et al., 2003; de Castro Araujo & Garcia, 2005). In nature, changes in phytoplankton community can modify both the quality and quantity of food in the food chain (Butler, 1994; Maazouzi et al., 2008; Whitehouse et al., 2008; Montes-Hugo et al., 2009).

The biochemical composition of algal species can vary significantly in their nutritional value. Clearly, environmental factors, particularly light, temperature, nutrient status, growth stage and salinity will affect the pathway and activity of cellular metabolism, as well as the cell composition (Shamsudin, 1992; Thompson et al., 1992a; Zhu et al., 1997; Renaud et al., 1994, 1995, 1999; Gatenby et al., 2003; Chen et al., 2008; Converti et al., 2009). Of all these factors, temperature is known to play major role in influencing the biochemical composition of algae (Goldman & Mann, 1980; Thompson et al., 1992a; de Castro Araujo & Garcia, 2005; Chen et al., 2008; Converti et al., 2009) as shown in Table 2. It seems most of the previous temperature studies documented only variation in carbon, nitrogen, and chlorophyll-a (Thompson et al., 1992a; Anning et al., 2001; Berges et al., 2002).

Growth temperature has strong influence on the changes of biochemical composition in algae. Overall, high growth temperature has been related to significant decrease in protein content, together with increases in lipid and carbohydrates (Tomaselli et al., 1988; Oliveira et al., 1999). For instance, Tomaselli et al. (1988) studied the influence of high temperature (40°C) on *Spirulina platensis* M2 cultivated continuously and observed a significant decrease in protein content (22%), together with a remarkable increase in lipids (43%) and carbohydrate contents (30%). However, opposite trend was found by other studies where high growth temperature has been associated with increases in protein content and decreases in carbohydrate (Thompson et al., 1992a), and lipid (Thompson et al., 1992a; Renaud et al., 1995) in some species.

It seems there is no consistent trend in proximate biochemical composition as a function of temperature. The response of biochemical composition to temperature variations was found to be species specific. For example, de Castro Araujo & Garcia (2005) found that higher lipid and carbohydrate content were obtained at lower temperatures (20 and 25°C) compared to high temperature (30°C) in diatom *Chaetoceros* cf.

wighamii, while protein content was unaffected. Another study on *Chaetoceros* sp. (Clone CS256) grown at 25°C contained higher lipid content, while for other species such as *Rhodomonas* sp., *Cryptomomas* sp. and *Isochrysis* sp. higher concentrations were observed at higher temperatures between 27 and 30°C (Renaud et al., 2002). All four tropical Australian species tested showed significantly lower percentage of protein content when cells were grown at temperatures above 27°C and there was no consistent trend in the percentage of carbohydrate as a function of temperature (Renaud et al., 2002). At lower temperature (< 15ºC), all eight species of marine phytoplankton increased their protein per cell but there is no consistent pattern in lipid and carbohydrate per cell as a function of temperature.

Two of the *Chaetoceros* species (*C. simplex* and *C. gracilis*) showed steady declines in lipid per cells as temperature increased from 10 to 25ºC. *Thalassiosira pseudonana*, *Phaeodactylum tricornutum*, and *Pavlova lutheri* all had minimums in lipid per cell at intermediate temperatures (15ºC) (Thompson et al., 1992a). In *Dunaliella tertiolecta* and *Isochrysis galbana*, protein content increases markedly when grown at temperatures higher than 15 ºC (Thompson et al., 1992a).

According to Zhu et al. (1997), the biochemical composition of the haptophyte *Isochrysis galbana* TK1 grown at 15 and 30°C varied at the two culture temperatures. The highest protein and carbohydrate contents were found at 15°C, while lipid content was higher at 30°C than at 15°C. In another study, it was found that the lipid content of *Nannochloropsis oculata* almost doubled when an increase in temperature from 20 to 25°C. However, an increase from 25 to 30°C caused a decrease of the lipid content of *Chlorella vulgaris* from 14.71 to 5.90% (Converti et al., 2009).

CONCLUSION

As demonstrated here, temperature plays an important role in controlling the physiological and biochemical processes in algae. The basic understanding on how algae respond and adapt to temperature change is crucial. However, most authors found that the response of algae to temperature changes varied with species. Temperature changes also determine species abundance and distribution of algae. As all organisms in the food chain are closely linked, it is of great significance to study the impact of algae at species level and relate the findings to the ecosystem.

ACKNOWLEDGEMENT

The authors gratefully acknowledge the grant from the Ministry of Science, Technology and Innovation (MOSTI), Malaysia coordinated by the Academy of Sciences Malaysia (ASM). The first author would like to thank MOSTI for the Pasca Postgraduate Fellowship.

REFERENCES

1. Ahlgren, G. (1987). Temperature functions in biology and their application to algal growth constants. *Oikos. 49*, 177 – 190.
2. Anning T., Harris, G., & Geider, R.J. (2001). Thermal acclimation in the marine diatom *Chaetoceros calcitrans* (Bacillariophyceae). *European Journal of Phycology, 36*, 233 – 241.
3. Beardall, J., & Raven, J.A. (2004). The potential effects of global climate change on microalgal photosynthesis, growth and ecology. *Phycologia, 43*, 26 – 40.
4. Beardall, J., & Stojkovic, S. (2006). Microalgae under global environmental change: implications for growth and productivity, populations and trophic flow. *ScienceAsia, 32*, 1 – 10.
5. Beardall, J., Stojkovic, S., & Larsen, S. (2009). Living in a high CO_2 world: impacts of global climate change on marine phytoplankton. *Plant Ecology and Diversity, 2*, 191 – 205.
6. Behrenfeld, M.J., Randerson, J.T., McClain, C.R., Feldman, G.C., Los, S.O., Tucker, C.J., Falkowski, P.G., Field, C.B., Frouin, R., Esaias, W.E., Kolber, D.D., & Pollack, N.H. (2001). Biospheric primary production during an ENSO transition. *Science, 291*, 2594 – 2597.
7. Berges, J.A., Varela, D.E., & Harrison, P.J. (2002). Effects of temperature on growth rate, cell composition and nitrogen metabolism in the marine diatom *Thalassiosira pseudonana* (Bacillariophyceae). *Marine Ecology Progress Series, 225*, 139 – 146.
8. Bischoff, B., & Wiencke, C. (1995). Temperature adaptation in strains of the amphi-equatorial green alga *Urospora penicilliformis* (Acrosiphoniales): biogeographical implications. *Marine Biology, 122*, 681 – 688.
9. Bischoff-Basman, B., Bartsch, I., Xia, B.M., & Wiencke, C. (1997). Temperature responses of macroalgae from the tropical island Hainan (P.R. China). *Phycological Research, 45,* 91 – 104.
10. Butler, N.M. (1994). Lipid storage in *Diaptomus kenai* (Copepoda; Calanoida):

effects of inter- and intraespecific variation in food quality. *Hydrobiologia, 274*, 9 – 16.
11. Butterwick, C., Heaney, S.I., & Talling, J.F. (2005). Diversity in the influence of temperature on the growth rates of freshwater algae, and its ecological relevance. *Freshwater Biology, 50*, 291 – 300.
12. Chailakhan, R., Khonsarn, N., Chirasuwan, N., Ruengjitchatchawalya, M., Bunnag, B., & Tanticharoen, M. (2007). Response of *Spirulina platensis* C1 to high temperature and high light intensity. *Kasetsart Journal (Natural Science), 41*, 123 – 129.
13. Chen, G.Q., Jiang, Y., & Chen, F. (2008). Variation of lipid class composition in *Nitzschia laevis* as a response to growth temperature change. *Food Chemistry, 109,* 88 – 94.
14. Chevalier, P., Proulx, D., Lessard, P., Vincent, W.F., & de la Noüe, J. (2000). Nitrogen and phosphorus removal by high latitude mat-forming cyanobacteria for potential use in tertiary wastewater treatment. *Journal of Applied Phycology, 12*, 105 – 112.
15. Chu, W.L., Phang, S.M., Goh, S.H., & Blakebrough, N. (1994). Environmental effects on growth and biochemical composition of *Ankistrodesmus convolutus*. *Proceedings of the Conference on Algal Biotechnology in the Asia-Pacific Region*, University Malaya, Kuala Lumpur, Malaysia, 16 – 27.
16. Chu, W.L., Wong, C.Y., Teoh, M.L., & Phang, S.M. (2005). Response and adaptation of algae to the changing global environment. In F. Kasai, K. Kaya & M.M. Watanabe (Eds.). *Algae Culture Collections and the Environment* (pp. 177 – 195). Japan: Tokai University Press.
17. Converti, A., Casazza, A.A., Ortiz, E.Y., Perego, P., & Del Borghi, M. (2009). Effect of temperature and nitrogen concentration on the growth and lipid content of *Nannochloropsis oculata* and *Chlorella vulgaris* for biodiesel production. *Chemical Engineering and Processing, 48*, 1146 – 1151.
18. Cyril, J., Powell, G.L., Duncan, R.R., & Baird, W.V. (2002). Changes in membrane polar lipid fatty acids of seashore paspalum in response to low temperature exposure. *Crop Science, 42,* 2031 – 2037.
19. de Castro Araujo, S., & Garcia, V.M.T. (2005). Growth and biochemical composition of the diatom *Chaetoceros* cf. *wighamii* brightwell under different temperature, salinity and carbon dioxide levels. I. Protein, carbohydrate and lipids. *Aquaculture, 246*, 405 – 412.
20. Eddie, B., Krembs, C., & Neuer, S. (2008). Characterization and growth response to temperature and salinity of psychrophilic, halotolerant *Chlamydomonas* sp. ARC isolated from Chukchi Sea ice. *Marine Ecology Progress Series, 354*, 107 – 117.
21. Eppley, R.W. (1972). Temperature and phytoplankton growth in the sea. *Fishery Bulletin, 70*, 1063 – 1085.
22. Falkowski, P.G., & Raven, J.A. (2007). *Aquatic photosynthesis* (2nd ed.). Princeton, NJ: Princeton University Press.
23. Fritsen, C.H., & Priscu, J.C. (1998). Cyanobacterial assemblages in permanent ice covers on Antarctic lakes: distribution, growth rate, and temperature response of photosynthesis. J*ournal of Phycology, 34,* 587 – 597.
24. Gacheva, G., & Pilarski, P. (2008). The resistance of a new strain *Chlorella* sp. R-06/2, isolated from an extreme habitat to environmental stress factors. *General and Applied Plant Physiology, 34*, 347 – 360.
25. Gatenby, C.M., Orcutt, D.M., Kreeger, D.A., Parker, B.C., Jones, V.A., & Neves, R.J. (2003). Biochemical composition of three algal species proposed as food for captive freshwater mussels. *Journal of Applied Phycology, 15,* 1 – 11.
26. Goldman, J.C., & Mann, R. (1980). Temperature influenced variations in speciation and the chemical composition of marine phytoplankton in outdoor mass cultures. *Journal of Experimental Marine Biology and Ecology, 46*, 29 – 40.
27. Harwood, J.L. (1988). Fatty acid metabolism. *Annual Review of Plant Physiology and Plant Molecular Biology, 39*, 101 – 138.
28. Hendriks, I.E., van Duren, L.A., & Herman, P.M.J. (2003). Effect of dietary polyunsaturated fatty acids on reproductive output and larval growth of bivalves. *Journal of Experimental Marine Biology and Ecology, 296*, 199 – 213.
29. Hoham, R.W. (1975). Optimum temperatures and temperature ranges for growth of snow algae. *Arctic and Alpine Research,* 7, 13 – 24.
30. Hoham, R.W., Frey, F.M., Mohn, W.W., Felio, J.H., Todd, S., Duncan, J.E., & Banghart, J.B. (2008). Optimum growth temperatures of three species of green *Chloromonas* snow algae from Upstate New York and the White Mountains, Arizona. *Arctic, Antarctic and Alpine Research, 40,* 355 – 363.
31. Hostetler, S.W., & Small, E.E. (1999). Response of North American freshwater lakes to simulated future climates. *Journal of the*

American Water Resources Association, 35, 1625 – 1637.
32. Hu, H.H., & Gao, K.S. (2006). Response of growth and fatty acid compositions of *Nannochloropsis* sp. to environmental factors under elevated CO_2 concentration. *Biotechnology Letters, 28,* 987 – 992.
33. IPCC (2007). Climate Change 2007. In S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor & H. L. Miller. (Eds.), *The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge, UK: Cambridge University Press.
34. Jiang H., & Gao, K. (2004). Effects of lowering temperature during culture on the production of polyunsaturated fatty acids in the marine diatom *Phaeodactylum tricornutum* (Bacillariophyceae). *Journal of Phycology, 40,* 651 – 654.
35. Kitaya, Y., Xiao, L., Masuda, A., Ozawa, T., Tsuda, M., & Omasa, K. (2008). Effects of temperature, photosynthesis photon flux density, photoperiod and O_2 and CO_2 concentrations on growth rates of the symbiotic dinoflagellate, *Amphidinium* sp. *Journal of Applied Phycology, 20,* 737 – 742.
36. Kojima, T., & Harrison, B. (1998). *The carbon dioxide problem: Integrated energy and environmental policies for the 21st century.* Amsterdam: Gordon and Breach Science Publishers.
37. Larkindale, J., & Huang, B.R. (2004a). Changes of lipid composition and saturation level in leaves and roots for heat-stressed and heat-acclimated creeping bentgrass (*Agrostis stolonifera*). *Environmental and Experimental Botany, 51,* 57 – 67.
38. Li, W.K.W. (1980). Temperature adaptation in phytoplankton: cellular and photosynthetic characteristics. In P.G. Falkowski (Ed.), *Primary productivity in the sea* (pp. 259 – 279). New York: Plenum Press.
39. Lovejoy, C., Vincent, W.F, Bonilla, S., Roy, S., Martineau, M.J., Terrado, R., Potvin, M., Massana, R., & Pedros-Alio, C. (2007). Distribution, phylogeny, and growth of cold-adapted picoprasinophytes in Arctic seas. *Journal of Phycology, 43,* 78 – 89.
40. Maazouzi, C., Masson, G., Izquierdo, M.S., & Pihan, J.C. (2008). Midsummer heat wave effects on lacustrine plankton: variation of assemblage structure and fatty acid composition. *Journal of Thermal Biology, 33,* 287 – 296.
41. Mangelsdorf, K., Finsel, E., Liebner, S., & Wagner, D. (2009). Temperature adaptation of microbial communities in different horizons of Siberian permafrost-affected soils from the Lena Delta. *Chemie der Erde, 69,* 169 – 182.
42. McBride, B.B., Muller-Parker, G., & Jakobsen, H.H. (2009). Low thermal limit of growth rate of *Symbiodinium californium* (Dinophyta) in culture may restrict the symbiont to Southern populations of its host anemones (*Anthopleura* spp.; Anthozoa, Cnidaria). *Journal of Phycology, 45,* 855 – 863.
43. Milke, L.M., Bricelj, V.M., & Parrish, C.C. (2008). Biochemical characterization and nutritional value of three *Pavlova* spp. in unialgal and mixed diets with *Chaetoceros muelleri* for postlarval sea scallops, *Placopecten magellanicus*. *Aquaculture, 276,* 130 – 142.
44. Montagnes, D.J.S., & Franklin, D.J. (2001).Effect of temperature on diatom volume, growth rate, and carbon and nitrogen content: reconsidering some paradigms. *Limnology and Oceanography, 46,* 2008 – 2018.
45. Montes-Hugo, M., Doney, S.C., Ducklow, H.W., Fraser, W., Martinson, D., Stammerjohn, S.E., & Schofield, O. (2009). Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science, 323,* 1470 – 1473.
46. Morgan-Kiss, R.M., Ivanov, A.G., Modla, S., Czymmek, K., Huner, N.P.A., Priscu, J.C., Lisle, J.T. & Hanson, T.E. (2008). Identity and physiology of a new psychrophilic eukaryotic green alga, *Chlorella* sp., strain BI, isolated from a transitory pond near Bratina Island, Antarctica. *Extremophiles, 12,* 701 – 711.
47. Mortensen, S.H., Borsheim, K.Y., Rainuzzo, J.K., & Knutsen, G. (1988). Fatty acid and elemental composition of the marine diatom *Chaetoceros gracilis* Schutt. Effects of silicate deprivation, temperature and light intensity. *Journal of Experimental Marine Biology and Ecology, 122,* 173 – 185.
48. Muhling, M., Belay, A., & Whitton, B.A. (2005). Variation in fatty acid composition of *Arthrospira* (*Spirulina*) strains. *Journal of Applied Phycology, 17,* 137 – 146.
49. Murata, N., & Nishida, I. (1987). Lipids of blue-green algae (cyanobacteria). In P.K. Stumpf (Ed.), *The biochemistry of plants* (Vol. 9, pp. 315 – 347). San Diego, United States of America: Academic Press.
50. Murata, N., & Wada, H. (1995). Acyl-lipid desaturases and their importance in the

tolerance and acclimatization to cold of cyanobacteria. *Biochemical Journal, 308,* 1 – 8.

51. Nadeau, T.L., & Castenholz, R.W. (2000). Characterization of psychrophilic Oscillatorians (cyanobacteria) from Antarctic meltwater ponds. *Journal of Phycology, 36,* 914 – 923.
52. Nagashima, H., Matsumoto, G.I., Ohtani, S., & Momose, H. (1995). Temperature acclimation and fatty acid composition of an Antarctic *Chlorella*. *Proceedings of the NIPR Symposium on Polar Biology, 8,* 194 – 199.
53. Ng, M.W., Camerlengo, A., & Abd. Wahab, A.K. (2005). A study of global warming in Malaysia. *Jurnal Teknologi, 42(F),* 1 – 10.
54. Nishida, I., & Murata, N. (1996). Chilling sensitivity in plants and cyanobacteria: the crucial contribution of membrane lipids. *Annual Review of Plant Physiology and Plant Molecular Biology, 47*, 541 – 568.
55. Okuyama, H., Orikasa, Y., & Nishida, T. (2008). Significance of antioxidative functions of eicosapentaenoic and docosahexaenoic acids in marine microorganisms. *Applied and Environmental Microbiology, 74*, 570 – 574.
56. Oliveira, M.A.S., Monteiro, M.P., Robbs, P.G., & Leite, S.G. (1999). Growth and chemical composition of *Spirulina maxima* and *Spirulina platensis* biomass at different temperatures. *Aquaculture International, 7,* 261 – 275.
57. Pakker, H., Breeman, A.M., Prud'homme van Reine, W.F., & van den Hoek, C. (1995). A comparative study of temperature responses of Caribbean seaweeds from different biogeographic groups. *Journal of Phycology, 31*, 499 – 507.
58. Peck, L.S., Clark, M.S., Clarke, A., Cockell, C.S., Convey, P., William, H.W., III., Fraser, K.P.P., Johnston, I.A., Methe, B.A., Murray, A.E., Romisch, K., & Rogers, A.D. (2005). Genomics: applications to Antarctic ecosystems. *Polar Biology, 28,* 351 – 365.
59. Quadir, D.A., Shrestha, M.L., Khan, T.M.A., Ferdousi, N., Rahman, M., & Mannan, A. (2004). Variations of surface air temperature over land areas in and around the Bay of Bengal. *Natural Hazards*, *31*, 561 – 584.
60. Rajadurai, M., Poornima, E.H., Narasimhan, S.V., Rao, V.N.R., & Venugopalan, V.P. (2005). Phytoplankton growth under temperature stress: Laboratory studies using two diatoms from a tropical coastal power station site. *Journal of Thermal Biology, 30,* 299 – 305.
61. Raven, J.A., & Geider ,R.J. (1988). Temperature and algal growth. *New Phytologist, 110,* 441 – 461.
62. Regier, H.A., Holmes, J.A., & Pauly, D. (1990). Influence of temperature changes on aquatic ecosystems: an interpretation of empirical data. *Transactions of the American Fisheries Society, 119*, 374 – 389.
63. Renaud, S.M., Parry, D.L., & Thinh, L.V. (1994). Microalgae for use in tropical aquaculture. I: Gross chemical and fatty acid composition of twelve species of microalgae from the Northern Territory, Australia. *Journal of Applied Phycology, 6,* 337 – 345.
64. Renaud, S.M., Thinh, L.V., & Parry, D.L. (1999). The gross composition and fatty acid composition of 18 species of tropical Australian microalgae for possible use in mariculture. *Aquaculture, 170,* 147 – 159.
65. Renaud, S.M., Thinh, L.V., Lambrinidis, G., & Parry, D.L. (2002). Effect of temperature on growth, chemical composition and fatty acid composition of tropical Australian microalgae grown in batch cultures. *Aquaculture, 211,* 195 – 214.
66. Renaud, S.M., Zhou, H.C., Parry, D.L., Thinh, L.V., & Woo, K.C. (1995). Effect of temperature on the growth, total lipid content and fatty acid composition of recently isolated tropical microalgae *Isochrysis* sp., *Nitzschia closterium*, *Nitzschia paleacea*, and commercial species *Isochrysis* sp. (clone T.ISO). *Journal of Applied Phycology, 7,* 595 – 602.
67. Robledo, D., & Freile-Pelegrin, Y. (2005). Seasonal variation in photosynthesis and biochemical composition of *Caulerpa* spp. (Bryopsidales, Chlorophyta) from the Gulf of Mexico. *Phycologia, 44,* 312 – 319.
68. Sandnes, J.M., Kallqvist, T., Wenner, D., & Gislerod, H.R. (2005). Combined influence of light and temperature on growth rates of *Nannochloropsis oceanica*: linking cellular responses to large-scale biomass production. *Journal of Applied Phycology, 17,* 515 – 525.
69. Sargent, J.R., Henderson, R.J., & Tocher, D.R. (1989). The lipids. In: H. Halver (Ed.), *Fish Nutrition* (Vol. 2, pp. 153 – 218). London: Academic Press.
70. Sato, N., Sonoike, K., Kawaguchi, A., & Tsuzuki, M. (1996). Contribution of lowered unsaturation levels of chloroplast lipids to high temperature tolerance of photosynthesis in *Chlamydomonas reinhardtii*. *Journal of Photochemistry and Photobiology, 36,* 333 – 337.

71. Seaburg, K.G., Parker, B.C., Wharton, R.A., & Simmons, G.M. (1981). Temperature-growth responses of algal isolates from Antarctic oases. *Journal of Phycology, 17,* 353 – 360.
72. Shamsudin, L. (1992). Lipid and fatty acid composition of microalgae used in Malaysian aquaculture as live food for the early stage of penaeid larvae. *Journal of Applied Phycology, 4,* 371 – 378.
73. Singh, V., Singh, B., & Goyle, M.R. (1994). Influence of temperature on cell biomass and biochemical composition of the thermophilic cyanobacterium, *Mastigocladus laminosus*. *Phykos, 33,* 59 – 65.
74. Smith, R.E.H., Stapleford, L.C., & Ridings, R.S. (1994). The acclimated response of growth, photosynthesis, composition, and carbon balance to temperature in the psychrophilic ice diatom *Nitzschia seriata*. *Journal of Phycology, 30,* 8 – 16.
75. Staehr, P.A., & Birkeland, M.J. (2006). Temperature acclimation of growth, photosynthesis and respiration in two mesophilic phytoplankton species. *Phycologia, 45,* 648 – 656.
76. Sushchik, N.N., Kalacheva, G.S., Zhila, N.O., Gladyshev, M.I., & Volova, T.G. (2003). A temperature dependence of the intra- and extracellular fatty-acid composition of green algae and cyanobacterium. *Russian Journal of Plant Physiology (English Translation), 50,* 374 – 380.
77. Sutherland, D.L. (2009). Microbial mat communities in response to recent changes in the physiochemical environment of the meltwater ponds on the McMurdo Ice Shelf, Antarctica. *Polar Biology, 32*, 1023 – 1032.
78. Suzuki, Y., & Takahashi, M. (1995). Growth response of several diatom species isolated from various environments to temperature. *Journal of Phycology, 31*, 880 – 888.
79. Tang, E.P.Y., & Vincent, W.F. (1999). Strategies of thermal adaptation by high-latitude cyanobacteria. *New Phytologist, 142,* 315 – 323.
80. Tang, E.P.Y., & Vincent, W.F. (2000). Effects of daylength and temperature on the growth and photosynthesis of an Arctic cyanobacterium, *Schizothrix calcicola* (Oscillatoriaceae). *European Journal of Phycology, 35,* 263 – 272.
81. Tang, E.P.Y., Tremblay, R., & Vincent, W.F. (1997a). Cyanobacterial dominance of polar freshwater ecosystems: are high-latitude mat-formers adapted to low temperature? *Journal of Phycology, 33*, 171 – 181.
82. Tang, E.P.Y., Vincent, W.F., Proulx, D., Lessard, P., & de la Noue, J. (1997b). Polar cyanobacteria versus green algae for tertiary waste-water treatment in cool climates. *Journal of Applied Phycology, 9*, 371 – 381.
83. Tangang, F.T., Juneng, L., & Ahmad, S. (2007). Trend and interannual variability of temperature in Malaysia: 1961 – 2002. *Theoretical and Applied Climatology, 89*, 127 – 141.
84. Tedesco, M.A., & Duerr, E.O. (1989). Light, temperature and nitrogen starvation effects on the total lipid and fatty acid content and composition of *Spirulina platensis* UTEX 1928. *Journal of Applied Phycology, 1,* 201 – 209.
85. Teoh, M.L., Chu, W.L., Marchant, H. & Phang, S.M. (2004). Influence of culture temperature on the growth, biochemical composition and fatty acid profiles of six Antarctic microalgae. *Journal of Applied Phycology*, *16*, 421 – 430.
86. Thompson, P.A., Guo, M., & Harrison, P.J. (1992a). Effects of temperature. I. On the biochemical composition of eight species of marine phytoplankton. *Journal of Phycology, 28,* 481 – 488.
87. Thompson, P.A., Guo, M., Harrison, P.J., & Whyte, J.N.C. (1992b). Effects of variation in temperature. II. On the fatty acid composition of eight species of marine phytoplankton. *Journal of Phycology, 28,* 488 – 497.
88. Tomaselli, L., Giovannetti, L., Sacchii, A., & Bochi, F. (1988). Effects of temperature on growth and bichemical composition in *Spirulina platensis* strain M2. In T. Stadler, J. Mellion, M.C. Verdus, Y. Karamanos, H. Morvan & D. Christiaen (Eds.), *Algal Biotechnology* (pp. 303 – 314). London: Elsevier Applied Science.
89. Wada, H., & Murata, N. (1990). Temperature-induced changes in the fatty acid composition of the cyanobacterium, *Synechocystis* PCC6803. *Plant Physiology, 92*, 1062 – 1069.
90. White, P.L., Wynn-Williams, D.D., & Russell, N.J. (2000). Diversity of thermal responses of lipid composition in the membranes of the dominant culturable members of an Antarctic fellfield soil bacterial community. *Antarctic Science, 12,* 386 – 393.
91. Whitehouse, M.J., Meredith, M.P., Rothery, P., Atkinson, A., Ward, P., & Korb, R.E. (2008). Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: Forcings, characteristics and implications for lower trophic levels. *Deep-Sea Research I, 55*, 1218 – 1228.

92. Wong, C.Y., Chu, W.L., Marchant, H., & Phang, S.M. (2007). Comparing the response of Antarctic, tropical and temperate microalgae to ultraviolet radiation (UVR) stress. *Journal of Applied Phycology*, *19*, 689 – 699.
93. Zhu, C.J., Lee, Y.K., & Chao, T.M. (1997). Effects of temperature and growth phase on lipid and biochemical composition of *Isochrysis galbana* TK1. *Journal of Applied Phycology*, *9*, 451 – 457.