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Fatty acids in microalgae and cyanobacteria in a changing world: Contrasting temperate and cold environments

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Abstract: Under the present changing climate conditions and the observed temperature increase, it is of high importance to understand its effects on aquatic microbial life, and organisms' adaptations at the biochemical level. To adjust to temperature or salinity stress and avoid cell damage, organisms alter their degree of fatty acids (FAs) saturation. Thus, temperature is expected to have strong effects on both the quantity and quality of FAs in aquatic microorganisms. Here we review some recent findings about FAs sensitivity to climate change in contrasting environments. Overall, heat waves may induce changes in the relative abundance of polyunsaturated FAs (PUFA). However, the impact of the exposure to warming waters is different in temperate and polar environments. In cold marine waters, high concentration of omega-3 (ω3) FAs such as eicosapentaenoic acid (EPA) is promoted due to the activation of the desaturase enzyme. In this way, cells have enough energy to produce or activate antioxidant protection mechanisms and avoid oxidative stress due to heat waves. Contrastingly, under high irradiance and heat wave conditions in temperate environments, photosystems' protection is achieved by decreasing EPA concentration due to desaturase sensitivity. Essential FAs are transferred in aquatic food webs. Therefore, any alteration in the production of essential FAs by phytoplankton (the main source of ω3) due to climate warming can be transferred to higher trophic levels, with cascading effects for the entire aquatic ecosystem.

Introduction

Increasing fossil fuel emissions during the past decades have increased atmospheric CO_2 concentrations and lead to a rise of global average temperatures (Myhre *et al.*, 2015; Abhilash, 2015). The average surface temperature of the planet increased around 1°C during 2019, being the second warmest year in the 140-year record (NOAA, 2020). Temperature is expected to further increase globally with larger changes at higher latitudes (Perkins-Kirkpatrick and Gibson, 2017). Predictions made by the Intergovernmental Panel on Climate Change (IPCC, 2019) indicate that the surface temperature would increase approximately from 3 to 5°C by 2100. Furthermore, the average ocean temperature increased by 0.06°C per decade in the last 50 years (Lindsey and Dahlman, 2017). As a result of the increased surface and air temperatures and the frequency of extreme heat days, the marine and freshwater temperatures will also continue to rise (IPCC, 2019).

Aquatic ecosystems such as large shallow lakes are particularly vulnerable to climate change (van Doorslaer *et al.*, 2007). For example, it could produce substantial coastline changes (Pussella *et al.*, 2015). However, the increases in temperature vary regionally.

The physico-chemical properties of polar environments are shifting rapidly, especially in the Arctic and in areas around the Antarctic Peninsula. In the Arctic Ocean, a 2°C increase was observed over the last 20 years (Economist, 2013). Temperature records for the West Antarctic Peninsula

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(WAP) have shown the largest average atmospheric warming in the Southern Hemisphere, accompanied by significant warming of surface and deeper waters, salinity changes and rapid glaciers retreat (Henley *et al.*, 2019). Moreover, marine ecosystems will be affected depending on the duration and intensity of the heat wave (Frölicher and Laufkötter, 2018) and the capacity of marine biota to adapt their physiology to the exposure to altered conditions (Doney *et al.*, 2012).

In the marine realm, a number of environmental factors determine the productivity of phytoplankton assemblages, many of which are affected by global climate change, ozone depletion and pollution (Winder and Sommer, 2012; Häder and Gao, 2015; Häder *et al.*, 2015). Temperature is a crucial factor, which controls growth and productivity through phytoplankton photosynthesis (Thyssen *et al.*, 2011; Raymont, 2014; Hernando *et al.*, 2015). In this manner, productivity shows a positive correlation with the increase in temperature up to species optimum (Huertas *et al.*, 2011). Changes in species composition are already being observed in response to altered temperature patterns (Larsson *et al.*, 2015; Hernando *et al.*, 2015, 2020; Antoni *et al.*, 2020), considering that the ability to adapt to such changes are species-specific in a phytoplankton assemblage (Gao *et al.*, 2012). Consequently, the pronounced variability in ocean-atmosphere exchanges of heat along WAP has a strong impact on primary production, community composition and ecosystem functioning (Ducklow *et al.*, 2013; Meredith *et al.*, 2017; Hernando *et al.*, 2015).

In freshwater systems, high inputs of nutrients usually favor phytoplankton growth and photosynthesis (Falkowski *et al.*, 1998; Behrenfeld *et al.*, 2006), which promoted an increase in the frequency of cyanobacterial blooms in the last decades. Additionally, warmer temperatures and eutrophication are often proposed as principal factors favoring these events (Chorus and Bartram, 1999; Paerl and Huisman, 2008). These blooms are further associated with a decrease in phytoplankton diversity (Oliver and Gand, 2000). Other environmental factors promoting the predominance of cyanobacteria are irradiance conditions (with optimum values between spring and autumn), the ability to fix atmospheric nitrogen, high pH (6.5 to 8.5), low rate of filtration by zooplankton and the ability to form gas vesicles (Martin, 2000; Paerl and Huisman, 2008).

Cyanobacteria are an excellent source of peptides, FAs, amino acids, vitamins, minerals and pigments (Mimouni *et al.*, 2012). On the other hand, diatoms are the most abundant phytoplankton species and major primary producers in the oceans and are recognized as the most ecologically successful microalgae (Obata *et al.*, 2013). Diatom's membranes are usually enriched with medium-chain FAs as well as very long chain polyunsaturated fatty acids (PUFA) (Zulu *et al.*, 2018). These unsaturated FAs (UFAs) play vital roles in membrane physiology. In addition, the ratio of UFAs to saturated FAs (SFA) determines membrane fluidity, which promotes several cellular activities (Altabe *et al.*, 2013). The optimal membrane fluidity to sustain physiological homeostasis is achieved by upward or downward regulation of UFAs synthesis ('homeoviscous adaptation', Hazel, 1995). Temperature stress may induce changes in the FAs of cell membranes to avoid damage and be protected against the effects of increased temperature (de la Rosa *et al.*, 2020). This adaptation allows cyanobacteria and microalgae such as diatoms to survive in extreme conditions and involves remodeling membrane lipids by modifying FAs chain length and unsaturation to sustain the desired level of fluidity in cell membranes (Sinensky, 1974).

Changes in PUFA in response to environmental stressors are highly relevant for the ecological role of cyanobacteria and microalgae as food sources for grazers and can therefore have serious implications for the flow of energy and the overall functioning of the ecosystem (Twining *et al.*, 2021).

The study of the changes induced by elevated seawater temperature in FAs and lipid metabolism enzymes of diatoms can provide insight into the impacts of marine heat waves on these organisms and on the potential repercussions on the entire marine food webs and ecosystems (Galloway and Winder, 2015). Changes in FAs metabolism and alterations in the expression of key genes (An *et al.*, 2013; Shimojima *et al.*, 2009) could be a response to environmental stresses such as heat waves.

Overall, organisms' responses to heat waves may involve reversible adjustment of their physiology by changing the content of some biomolecules or with activation of antioxidant systems, among other processes (Hernando *et al.*, 2015; Hernando *et al.*, 2018; Hernando *et al.*, 2020; de la Rosa *et al.*, 2020). Because phytoplankton growth and composition are highly dependent on environmental conditions (Galloway and Winder, 2015; Antoni *et al.*, 2020), there is an urgent need to understand how microalgae will be affected at the biochemical level in our warming world. Also, algae inhabiting regions at different latitudes are adapted to different ranges of temperatures.

The aim of this review is to compare the microalgae and cyanobacteria response from cold *vs.* temperate and tropical waters, to heat waves in relation to climate change and summarize the mechanisms of action leading to the observed FAs changes.

Importance of Fatty Acids and Their Role in Ecosystems

There are two major groups of FAs: SFA and UFAs, which differentiate from each other by the existence of double bonds in UFAs. The position of the double bonds is determined by the desaturase enzyme activity, which performs its activity in different positions accordingly to the type of enzyme present in different organisms (Brett and Müller-Navarra, 1997). SFA are mainly considered a source of energy and lipid storage. UFAs can be identified by the number of double bonds: Monounsaturated FAs (MUFAs) have one double bond and can be synthesized *de novo* almost by all organisms (Arts *et al.*, 2001). PUFA are FAs of 18 carbons or more in length with two or more double bonds. They can be classified into n–6 (or ω6) and n–3 (or ω3) major groups, depending on the position of the first double bond proximate to the methyl end of the FAs.

FAs synthesis in algae occurs through an aerobic pathway (Monroig *et al.*, 2013), it takes place in the chloroplast and the endoplasmic reticulum (ER). The glucose produced by photosynthesis is converted by glycolysis to pyruvate, which is the molecular basis for all metabolism processes. The desaturation and elongation process takes place in the ER. It uses 18:1ω9 to form linoleic

acid (LA; 18:2ω6) by Δ12 desaturase and further into either the ω6 pathway by Δ6 desaturase or into the ω3 pathway by Δ15 desaturase to form alpha-linolenic acid (ALA; 18:3ω3). Different organisms utilize a diverse amount of desaturases to come to the different PUFA as shown in Fig. 1.

In consumers, PUFA play an essential role in brain development (Liu *et al.*, 2015) and many physiological functions such as down regulating inflammation and cellular signaling (Stillwell and Wassall, 2003). Essential FAs are some PUFA that play major important functions in physiological and biochemical processes. These must be acquired through dietary input, considering that the majority of the animals cannot synthesize them *de novo* (Kattner and Hagen, 2009) due to the lack of the desaturase enzyme (Sargent *et al.*, 1993).

Phytoplankton accounts for nearly 50% of net primary production on Earth, and is the source of many biomolecules (Field *et al.*, 1998) such as FAs (Guschina and Harwood, 2009) which are crucial components of the biosphere (Beardall *et al.*, 2009). PUFA play an important role in the food web because they affect key physiological processes and are precursors to many hormones (Jónasdóttir *et al.*, 2009; de Troch *et al.*, 2012). Thus, PUFA are critical regulators of the survival, reproduction, and

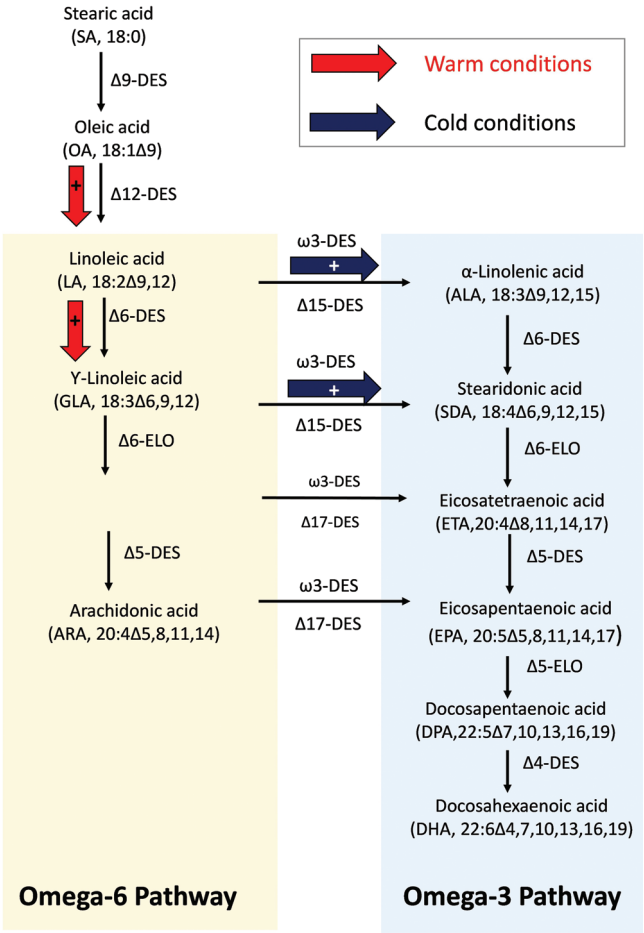

FIGURE 1. Simplified desaturation pathway of the FAs synthesis in phytoplankton cells. Des: Desaturase, Elo: elongase. Modified from Jónasdóttir *et al.* (2009) and Vaezi *et al.* (2013). The arrows indicate potential changes in the ω6 and ω3 FAs production path as a function of temperature. Red and black arrows indicate high or low temperature conditions, respectively.

population growth in invertebrates and fish (Copeman *et al.*, 2002; Von Elert, 2004).

Long-chain ω3 FAs, particularly eicosapentaenoic acid (EPA, 20:5ω3), docosapentaenoic acid (DPA, 22:5ω3), and docosahexaenoic acid (DHA, 22:6ω3) have been specially studied due to their important physiological functions and because the human body is unable to synthesize these compounds *de novo* (Drouin *et al.*, 2019). The brain has a high content of DHA, representing 50% of the total brain lipid and 10–15% of all of the FAs (Diau *et al.*, 2005). EPA was also found to be present at low concentrations in the brain (Chen *et al.*, 2009) probably because it rapidly converts to DHA (Kaur *et al.*, 2010). EPA in the brain provides important anti-inflammatory and immunity functions, but also plays an important role in neurotransmission and synaptic plasticity (Tassoni *et al.*, 2008; Uauy *et al.*, 2000).

In general terms, lipids produced by phytoplankton provide energy and essential nutrients for consumers in aquatic (Guschina and Harwood, 2009; Parrish, 2013) and terrestrial ecosystems (Gladyshev *et al.*, 2009; Hixson *et al.*, 2015). The herbivorous zooplankton and the fish that prey on them cannot synthesize all the FAs or cannot synthesize them in amounts required for optimal physiological performance (Brett *et al.*, 2006; Arts *et al.*, 2009). Hence, consumers acquire the required essential FAs from dietary lipids supplied by phytoplankton FAs, for example, LA, ALA, EPA, arachidonic acid (ARA, 20:4ω6) and DHA. In addition to their nutritive role, lipids form the backbone of the lipid bilayer in cell membranes (Arts *et al.*, 2009; Parrish, 2013). Although microalgae are the primary producers of EPA and DHA in marine food webs, humans use marine fish oil as the principal source of these PUFA (Sinclair, 2000). Moreover, the marine fish industry is increasingly declining due to overfishing and environmental pollution, while the production costs of DHA or EPA from cultured algae are potentially equal to the cost of producing EPA from fish oil (Milledge, 2011) and lower than the costs of PUFA from shellfish flesh and by-products (Al Khawli *et al.*, 2019; Dvoretsky *et al.*, 2021). Different algal taxa exhibit different FAs profiles (Harwood, 1998; Napolitano, 1999) as shown in Table 1 and Fig. 2). Jónasdóttir (2019) revealed a phyla-specific, and a highly species-specific PUFA production of marine phytoplankton, showing that the highest proportion of PUFA is found in Chlorophyta and Cryptophyta, and the lowest in Ochrophyta, Cyanobacteria and diatoms (Maltse and Maltseva, 2021). Diatoms are an important nutrition source in the marine environment, since many species produce large quantities of EPA (Arao *et al.*, 1987; Dunstan *et al.*, 1994). Both EPA and DHA are particularly found in diatoms, dinoflagellates and prymnesiophytes (Tonon *et al.*, 2002; Mansour *et al.*, 2005), they are produced from their precursor, ALA which is considered an essential FAs (Cook and McMaster, 2004).

Some ω3 are mainly synthesized by producers in aquatic environments (Hixson *et al.*, 2015; Twining *et al.*, 2015). These PUFA are progressively consumed and selectively retained by other aquatic organisms higher up in the food chain (Kainz *et al.*, 2004; Hixson *et al.*, 2015), and transferred to terrestrial ecosystems via consumption (Gladyshev *et al.*, 2009, 2013). Thus, PUFA composition of

TABLE 1

FAs composition in different edible marine and freshwater sources in cold and temperate environments

Region	Phytoplankton group/Species	Exposure conditions (Time/Stressor)	SFA	MUFA	PUFA	UFA/SFA	ω3 content at the end of experiments	Reference
Temperate	*Microcystis aeruginosa* (A)	7 days/T+	16:0; 18:0	cis-9-18:1	GLA; ALA	N/ch	↓	de la Rosa *et al.*, 2020
Antartic	*Chlamydomonas sp* (B)	56 hs/T (−20, −10, 0, 5°C)	16:0; 18:0	16:1	18:3; 20:5; 20:3	N/ch	↑	An *et al.*, 2013
Antartic	Diatoms, Prasinophytes, Cryptophytes, Prymnesiophytes and others (C)	6 days/S-T+; S0T+; S-T0	16:0; 14:0; 18:0	16:1ω7	16:3ω3; SDA; EPA; DHA	↑ (S-T+;S0T+)	↑ (S-T+; S0T+; S-T0)	Hernando *et al.*, 2018
Temperate	Diatoms and Green algae	T+	N/A	N/A	ALA; EPA; DHA; LA; ARA	N/A	↓	Arts *et al.*, 2015
Temperate	*Thalassiosira pseudonana* (D)	500 generations/T+ (16, 31°C)	16:0; 18:0	16:1Δ3; 16:1Δ7	EPA; DHA; 16:3ω3; 16:4ω3; ALA	N/A	N/A	O'Donnell *et al.*, 2019
Temperate	*Thalassiosira weissflogii* (E)	7 days/S0T+; S-T+; S+T+; S0T-; S+T-; S-T-; S0	23:0; 21:0; 20:0	16:1; 17:1	20:3ω3; ARA; EPA; DHA	↓ (S0T+; S+T+) ↑ (S0T-;S+T-;S-T-;S-T+)	↓ (S0T+;S+T+) ↑ (S0T-;S-T+;S-T-)	Gonçalves *et al.*, 2017
Temperate	*Scenedesmus obliquus* (F)	2 weeks/T+	16:0; 18:0	18:1ω9	LA; ALA; SDA	↓	↓	Fuschino *et al.*, 2011
Antartic	Coastal phytoplankton assemblage (C)	7 days/S0T0; S-T0;S0T+;S-T+	14:0; 16:0	16:1ω7	SDA; EPA	↑ (S0T+;S-T+)	↑ (S0T+;S-T+)	Antacli *et al.*, 2021
Temperate	*Nannochloropsis sp.* (G)	7 days/L+S+, L+S0, L+S-, L-S+, L-S0, L-S-	16:0; 14:0	16:1; 18:1ω9	LA; ARA; EPA	N/A	↑ low salinity, independent of light intensity	Pal *et al.*, 2011
Polar	*Chaetoceros brevis, Pyramimonas sp.* (H)	L-T+;L+T+; L-T-;L+T-	16:0	16:1ω7 (except *Pyramimonas sp.)*	SDA; 16:4 (EPA only in *C. brevis* and DHA only in *Pyramimonas sp.*)	N/A	↑	Boelen *et al.*, 2013
Temperate	*Thalassiosira weissflogii*, *Emiliania hux* and *Fibrocapsa japonica*	L-T+;L+T+; L-T0;L+T0	16:0; 14:0	16:1ω7 (except *E. hux*)	SDA (EPA except *E. hux* and DHA except *F. japonica*)	N/A	↓	

(Continued)

Table 1 (continued).

Region	Phytoplankton group/Species	Exposure conditions (Time/Stressor)	SFA	MUFA	PUFA	UFA/SFA	ω3 content at the end of experiments	Reference
Temperate	*Phaeodactylum tricornutum* (I), *Chaetoceros muelleri* (J)	2 h/T+ (30, 35, 40°C) and 24 h/T+ (30, 35°C)	16:0; 14:0	16:1	EPA	↓	↓	Rousch *et al.*, 2003
Temperate	*Phaeodactylum tricornutum* (I)	5 days/Heat waves (18, 26°C)	16:0; 14:0	16:1	18:2ω6; 18:3ω6; 20:3ω6; EPA; 18:4ω3; 16:3ω4	↓	↓	Feijão *et al.*, 2020
Antarctic	Sea-ice diatom *Nitzschia lecointei* (K)	7 days/S-T+ (–1.8; 3°C)	16:0; 14:0; 18:0	16:1ω7; 18:1ω9	18:3ω3; 18:4ω3; EPA; 22:6ω3	↑	↑	Torstensson *et al.*, 2019
Temperate	*Odontella aurita* (L)	10 days/8, 16, 24°C	14:0; 16:0; 18:0	16:1ω7; 18:1ω9	18:4ω3; 20:4ω6; EPA; 22:6ω3	↓	↓	Pasquet *et al.*, 2014
Tropical	*Chaetoceros sp.; Rhodomonas sp.; unidentified Prymnesiophyte* (M)	Exposed to 25, 27, 30 and 33°C. Harvested in late logarithmic grown phase	12:0; 14:0; 16:0; 17:0; 18:0	16:1ω7; 18:1ω9 18:1ω7	16:2ω7; 18:2ω6; 18:3ω6; EPA; 18:4ω3; 22:6ω3	↓	↓	Renaud *et al.*, 2002
Sub-tropical	*Nannochloropsis salina*(N)	14 days/17, 21 and 26°C	14:0; 16:0	16:1; 18:1ω9	20:4ω6; 18:2ω6; 18:3ω6; EPA	↓	↓	Hoffmann *et al.*, 2010
Polar	*Leptolyngbya sp.* (O)	Ambient conditions	18:0; 12:0; 17:0	16:1ω9; 18:1ω7	18:2ω6; 18:3ω6; 18:3ω3; EPA	N/A	N/A	Zainal Abidin *et al.*, 2020

Note: The effect of different treatments (increased temperature (T+), decreased salinity (S-), light conditions) are shown. N/A: not available; N/Ch: not significant changes; T: temperature; S: salinity; L: light intensity; 0: control; WT: wild type; ARA: arachidonic acid, 20:4ω6; GLA: gamma linolenic acid, 18:3ω6; ALA: alpha-linolenic acid, 18:3ω3; SDA: stearidonic acid, 18:4ω3; EPA: eicosapentaenoic acid, 20:5ω3; DHA: docosahexaenoic acid, 22:6ω3; LA: linoleic acid, 18:2ω6; POA: palmitoleic acid, 16:1Δ9.

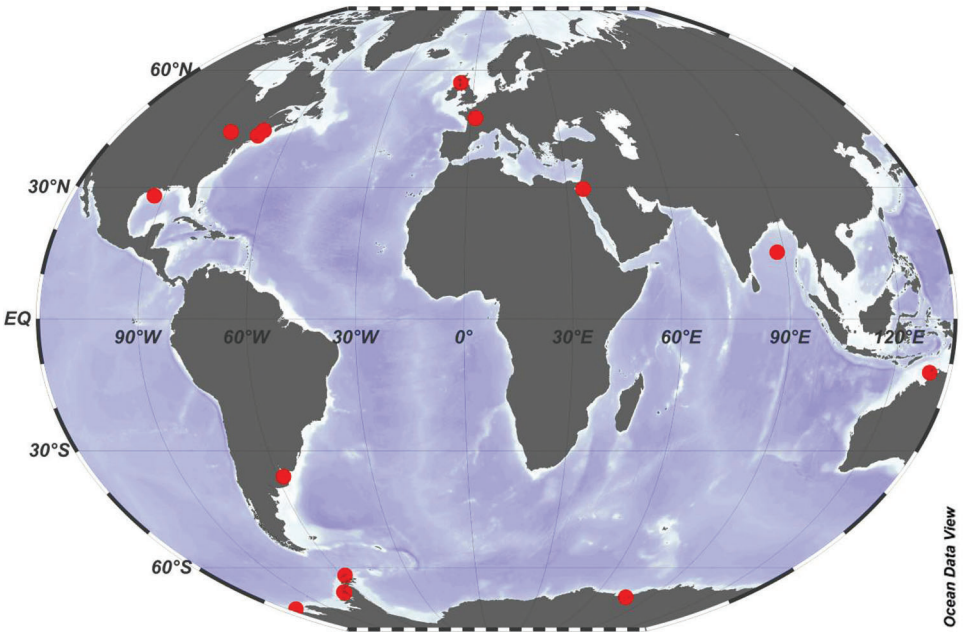

FIGURE 2. Distribution of studies on the effects of temperature increase on microalgae and cyanobacteria FAs composition. Red dots denote positioning and letters from the Roman alphabet correspond to the phytoplankton species or groups indicated in Table 1.

phytoplankton is an important determinant of food quality and, consequently, the health and optimal functioning of both aquatic and terrestrial consumers (Budge *et al.*, 2002; Dalsgaard *et al.*, 2003).

Changes in Membrane Fatty Acids

Temperature has strong directional effects on both the quantity and quality of FAs in phytoplankton. Phytoplankton and other organisms adapt to changing temperatures by modifying the structure of their membranes (Winter and Dzwolak, 2005), a process known as homeoviscous adaptation (see above). The double bonds in PUFA increase flexibility, leading to increased membrane fluidity. Under a sudden change in environmental conditions, *de novo* synthesis of UFAs cannot occur rapidly, but the desaturation of FAs may be adjusted by transferring specific acyl groups to other polar lipids and allowing rapid adaptive membrane reorganization (Khozin-Goldberg and Cohen, 2006). Temperature changes may then induce the replacement of an enzyme by an isoenzyme with better heat- or cold-tolerance (Steele and Fry, 2000). Several authors have shown an inverse relationship between temperature and FAs unsaturation in microalgae (Wada *et al.*, 1990; Zhu *et al.*, 1997).

PUFA represent between 30 and 60% of total FAs content in natural polar ocean assemblages and in individual phytoplankton species (Teoh *et al.*, 2004). Hernando *et al.* (2018) described the predominance of PUFA (44–64% in average) over SFA for Antarctic coastal phytoplankton at the beginning of microcosm experiments to evaluate the effects of increased temperature and decreased salinity on physiology (Table 1, Fig. 2).

In polar region, cyanobacteria mats from streams and lakes are dominated by Nostoc or oscillatorians (Oscillatoriaceae) (Zainal Abidin *et al.*, 2020) with extreme accumulations up to 90 cm thick and > 40 μg Chla cm^{-2} at some sites. Picocyanobacteria often dominate the phytoplankton in polar lakes achieving some of the highest natural concentrations on record, up to 8×10^6 cells mL^{-1} in some Antarctic lakes (Vincent, 2000). In marine waters in the Southern Ocean, picocyanobacteria were found to decrease during spring (Massana *et al.*, 1998) and summer (Murray *et al.*, 1998), and it has been speculated that the significant decline of archaea during spring/summer is a result of the competition with non-archaeal microorganisms during phytoplankton blooms (Massana *et al.*, 1998). Regarding FA studies in these organisms, Zainal Abidin *et al.* (2020) demonstrated a high content of UFAs in four of the five isolated species of the filamentous cyanobacterium *Leptolyngbya* sp. from fine Antarctic mats. The ω6 linoleic acid reached an average percentage of 60% followed by palmitoleic acid (10%) and oleic acid (10%) as shown in Table 1 and Fig. 2.

Contrarily to observations in Antarctic waters, Ohse *et al.* (2015) found in a FAs study with temperate marine species (*Nannochloropsis oculata*, *Thalassiosira pseudonana*, *Phaeodactylum tricornutum*, *Isochrysis galbana*, *Tetraselmis suecica*, *Tetraselmis chuii*, *Chaetoceros muelleri*, *Thalassiosira fluviatilis* and *Isochrysis* sp.) and the freshwater *Chlorella* sp, that average PUFA in these species was around 20%. Also, the cyanobacteria *Microcystis aeruginosa*, showed a PUFA relative abundance around 40% of the total FAs (de la Rosa *et al.*, 2020).

Water temperature is one of the most important factors in the regulation of PUFA synthesis by microalgae or cyanobacteria and their accumulation by zooplankton. Thus, global warming may lead to a decrease of PUFA in aquatic ecosystem (Thompson *et al.*, 1992; Renaud *et al.*, 2002; Maazouzi *et al.*, 2008) in order to maintain fluidity (see above). Conversely, acclimation to increasing temperature involves decreasing PUFA membrane content, while, simultaneously, increasing SFA (Rousch *et al.*, 2003; Fuschino *et al.*, 2011) as shown in Table 1.

Consequences of the Increase in Temperature in the Composition of FAS in Temperate and Tropical *vs.* Cold Environments

An important consequence of climate change is that increasing water temperatures are expected to reduce the

global production of PUFA in phytoplankton. The environment temperature and salinity affect the FA profile of microalgae, and it was found that DHA content decreases significantly with an increase in water temperature and salinity (Adarme-Vega *et al.*, 2012). Similarly, the EPA content was also found to decrease considerably with an increase in water temperature (Sang *et al.*, 2012). Changes in the biochemical composition of phytoplankton cell membranes may lead to cascading effects throughout the world's aquatic ecosystems. Further, such modified biochemical composition in aquatic ecosystems, as mentioned above, is also anticipated to propagate to terrestrial animals because of the flux of aquatic biomass, containing ω3 PUFA (Gladyshev *et al.*, 2009; Gladyshev *et al.*, 2013). This is critical because PUFA not only enhance the growth rates and reproductive capacities of aquatic animals (Ballantyne *et al.*, 2003), but are also vitally important to the neural/cognitive, cardiovascular, and visual health of terrestrial vertebrates (Calder, 2015).

Antarctic Waters

Rapid changes in temperature and salinity may have great effects on the physiology and biochemical composition of Antarctic diatoms. Hernando *et al.* (2018) and Antacli *et al.* (2021) demonstrated that EPA increased in Antarctic coastal phytoplankton assemblage in response to stress (increased temperature combined with freshening), in concordance with results from Teoh *et al.* (2013) as shown in Table 1 and Fig. 2. An *et al.* (2013) working with the Antarctic ice algae *Chlamydomonas* sp. and considering the FA desaturase (FADs) expression, demonstrated an increased amount of EPA in cells exposed to 0 and 5°C in comparison to controls at −10°C. This is related to the strategies adopted for survival at low temperatures, which include an increasing degree of FAs unsaturation or branching and a decrease in the FAs chain length (Penfield, 2008). An *et al.* (2013) results indicated that the mRNAs of FADs in *Chlamydomonas* sp. were regulated differentially in response to temperature stress. Moreover, those desaturases involved in ω3 production as shown in Fig. 1 were found to be sensitive to low temperature, indicating that they might play primary roles in protecting algal cells from potential damage at low temperature. Furthermore, when cells of the Antarctic sea-ice diatom *Nitzschia lecointei* were grown at 3°C, they had higher relative PUFA content (mainly hexadecatetraenoic [16:4ω4] and EPA) and lower relative MUFAs content than cells grown at −1.8°C (Torstensson *et al.*, 2019). Diatoms isolated from sea ice show a FAs composition characterized by high levels of EPA and C16 PUFA (Henderson *et al.*, 1998). Analysis of the FAs of a natural Arctic phytoplankton assemblage showed that, when dominated by diatoms of the genera *Thalassiosira* and *Chaetoceros*, the proportions of C16:1(ω7) and EPA were correspondingly high (Reuss and Poulsen, 2002).

Most algae produce EPA via the ω3 pathway as shown in Fig. 1. The biosynthesis of EPA occurs through a series of reactions that can be divided into two distinct steps. First is the *de novo* synthesis of oleic acid (OA, 18:1ω9) from acetate. OA is further desaturated by a Δ12 desaturase to form LA and a Δ15 desaturase to form ALA. Then, ω6 and ω3 FAs families are formed from their precursors by a series of desaturation and elongation reactions, including EPA as shown in Fig. 1. The three FAs, OA, LA and ALA, compete with each other for the D6 desaturase. The affinity of the enzyme to the substrate and the amount of substrate available determine which metabolic pathway is predominant (Gurr, 1985). Generally, the first Δ6 desaturation is the limiting step and ALA has the highest affinity for Δ6 desaturase followed by LA and oleic acid (Jónasdóttir, 2019). In order to enhance EPA production in *Dunaliella salina* (a green alga), FAs desaturares (Δ6) FADS6 from the diatom *Thalassiosira pseudonana*, Shi *et al.* (2018) constructed and overexpressed in *D. salina* with a plasmid (Ds-TpFADS6). They demonstrated that EPA production increased significantly in *D. salina transformants*. However, after Ds-TpFADS6 transformants were maintained at low temperature (4°C) for 5 days, their ALA levels increased but LA levels decreased. From this, they concluded that the activity of other desaturase enzymes overexpressed in *D. salina*, Ds-FADS15 (Δ15), was enhanced at low temperature, promoting the conversion of LA to ALA and increasing the ALA level as show in Fig. 1. These findings are similar to those of Okuda *et al.* (2015), who observed an accumulation of EPA in *Mortierella alpina* at low temperature (below 15°C). Ds-FADS15 and Ds-FADS6 in *M. alpine transformants* had high activity and exhibited greater EPA accumulation under varying temperatures than under constant temperatures, suggesting a more active LA-ALA-EPA pathway under these conditions. There was also less LA flux through the ω6 pathway as shown in Fig. 1.

EPA or other long-chain PUFA (LC-PUFA) may play a role in the functioning of the thylakoid membrane and are therefore essential for photosynthesis (Cohen *et al.*, 1988). At higher irradiance, photosynthesis is less efficient and thus fewer thylakoid membranes are required. As a result, LC-PUFA content could be lower in high light-acclimated algae (Harwood and Jones, 1989). Hence, cold-adapted polar microalgae could have high EPA and DHA production, since they can exhibit high growth rates under low temperature and irradiance conditions. Furthermore, polar species are expected to sustain a higher EPA and DHA content, since their habitat is characterized by lower average irradiance and temperature levels (Schloss *et al.*, 2002).

Changes in salinity may also modify the composition of FA and influence the physiological properties of microalgae (Hernando *et al.*, 2018). Due to the increase in the occurrence of heat waves in the WAP, melt water and seawater freshening increased. Xu and Beardall (1997) demonstrated that the content of ω3 in *Dunaliella* sp. decreased as the average salinity increased. In a culture of the marine diatom *Nitzschia laevis*, EPA yield was the highest at half the salinity of the artificial seawater (Wen and Chen, 2001). Similarly, both EPA and 18:4ω3 were significantly higher in natural Antarctic phytoplankton assemblages after 48 h exposure at salinities 4 PSU lower than environmental values (Hernando *et al.*, 2018).

High level of intracellular molecular oxygen may be another reason for the increased PUFA at low temperature, because the enzymes responsible for desaturation and elongation of PUFA depend on the availability of molecular

oxygen (Chen and Johns, 1991; Singh and Ward, 1997). A temperature shift strategy has been employed to enhance the overall ω3 PUFA production (including EPA) because the optimal temperature for microalgal growth is often higher than that for ω3 PUFA formation (Jiang and Chen, 2000). Such a phenomenon has been observed in many different algal species including *Porphyridium cruentum* (Springer *et al.*, 1994), *Nannochloropsis* sp. (Sukenik, 1991) and *P. irregulare* (Stinson *et al.*, 1991).

To the best of our knowledge, there are no studies testing the effects of temperature increase on FA of Antarctic cyanobacteria. In a recent latitudinal study, Breton *et al.* (2020) demonstrated that the distribution of marine *Synechococcus* cyanobacteria depends on the differentiation of lineages adapted to distinct thermal environments. Over the temperature gradient they sampled, all strains maintained efficient photosynthetic capacities. Subpolar and cold temperature strains actually showed enhanced capacities for lipid monodesaturation thanks to an additional Δ9-desaturase. By contrast, tropical and warm temperature strains displayed moderate monodesaturation capacities but high proportions of double unsaturations in response to cold temperatures, thanks to Δ12-desaturases. The desaturase genes displayed specific distributions directly related to latitudinal variations in ocean surface temperature. Thus, this study highlights the critical importance of membrane fluidity modulation by desaturases in the adaptive strategies.

Temperate and Tropical Waters

Many studies have shown changes in the FAs composition of microalgae and cyanobacteria from temperate waters when exposed to changes in temperature. *Phaeodactylum tricornutum* has been used as a model organism for diatom physiology studies, being the first pennate diatom to have its genome completely sequenced (Bowler *et al.*, 2008). It has been shown that this species has the ability to produce up to 35% of EPA of total FA (Hamilton *et al.*, 2014). The thylakoid membrane of *P. tricornutum* is composed of uncharged glycolipids such as monogalactosyldiacylglycerol (MGDG) and digalactosyldiacylglycerol (DGDG) (Yang *et al.*, 2017), with EPA being the most abundant component of the glycolipids (Mühlroth *et al.*, 2013). Jiang and Gao (2004) explained that elevated levels of UFAs in the diatom *P. tricornutum* after 12 h of exposure to low temperatures were due to increased activity of desaturase. Other studies have shown similar changes in the FA composition in diatoms within a similar period of time (12–48 h) (Tonon *et al.*, 2002; Siron *et al.*, 1989; Liang *et al.*, 2006). Thompson *et al.* (1992) who studied the effect of temperature over the range from 10 to 25°C on the FA composition of eight species of marine phytoplankton, including *Thalassiosira pseudonana* and three species within the genus *Chaetoceros* also showed a trend towards elevated PUFA at a lower temperature. However, only for *T. pseudonana* the percentage of DHA decreased linearly with increasing temperature. Blanchemain and Grizeau (1999) noted that the diatom *Skeletonema costatum* increased its EPA levels relative to dry weight at only the lowest (15°C) of three treatment temperatures and that there was a positive correlation between treatment duration (4 or 15 h) and EPA production at a particular temperature.

Species of the genus *Nannochloropsis* (Eustigmatophyceae, Monodopsidaceae) from sub-tropical sea waters are an important source of the essential EPA and are widely used in marine aquaculture nutrition (Renaud and Parry, 1994). The quality of *Nannochloropsis* biomass for aquaculture (high EPA percentage of total FAs) has been shown to deteriorate with culture age and with increasing light intensity, salinity level, and temperature. In addition, a concomitant increase in the proportions of saturated and monounsaturated fatty acids 14:0, 16:0, and 16:1 was found (Sukenik *et al.*, 1993; Renaud and Parry, 1994; Roncarati *et al.*, 2004). Hoffmann *et al.* (2010) also described this trend for *Nannochloropsis salina* with increased EPA contents under a low culture temperature (17°C) as compared to moderate temperatures of 21°C and 26°C (Table 1, Fig. 2).

Renaud *et al.* (2002) also demonstrated a decrease in the total production of the PUFA, including significant decreases in the percentages of the 20:5ω3 and 22:6ω3 in three tropical Australian species of *Rhodomonas* sp., an unidentified prymnesiophyte and a *Chaetoceros* sp. at higher growth temperatures between 33°C and 35°C when harvested during in late logarithmic growth phase. These results concurs with the findings of previous studies (Mortensen *et al.*, 1988; Renaud *et al.*, 1995) as shown in Table 1 and Fig. 2.

For the temperate *Chlamydomonas*, temperature stress (variation from optimum) caused an increase in SFA (Teoh *et al.*, 2013). The increase in SFA could be an important energy source for stress adaptation in these microalgae. The role of UFAs in membrane fluidity has been demonstrated in other algae such as *Spirulina platensis* (Sushchik *et al.*, 2003), *Chlamydomonas* sp. (Poerschmann *et al.*, 2004), and *C. vulgaris* strain BI (Morgan-Kiss *et al.*, 2008) when subjected to temperature stress. Pal *et al.* (2011) demonstrated that the eustigmatophyte *Nannochloropsis* sp. accumulate energy-rich storage products when exposed to unfavorable conditions that limit growth as long as the carbon supply exceeds the photosynthetic capacity of the cells. Also, low temperatures resulted in higher lipid production in *Nitzschia palea* (Renaud *et al.*, 1995), *Chaetoceros* sp. (Clone CS256) (Renaud *et al.*, 2002) and *Chaetoceros* cf. *wighamii* (de Castro Araujo and Garcia, 2005).

Qiao *et al.* (2016) found a higher DHA/EPA ratio in *P. tricornutum* grown under altered environmental conditions. DHA percentage increased with increasing light intensity, but decreased with increasing temperature. Furthermore, Feijão *et al.* (2017) also working with *P. tricornutum* from temperate ocean waters, demonstrated that cells exposed to heat wave conditions showed lower relative EPA contents and double bond indexes, whereas the ω6/ω3 ratio increased like in the cyanobacteria *Microcystis aeruginosa* (de la Rosa *et al.*, 2020). Moreover, the analysis of the FAs profiles in *P. tricornutum* also suggested that heat exposure negatively impacted thylakoid lipids, in agreement with the decrease observed in photosynthesis. Oxygen-evolving complexes are essential for the water splitting reaction occurring at the donor side of the photosystem II (PSII) and essential not only for oxygen production but also for fueling the quinone pool with the necessary energy for electron transport from

PSII to PSI (Strasser *et al.*, 2000). These complexes are usually heat-sensitive (Duarte *et al.*, 2016) and therefore heat waves may have a negative impact on photosynthesis and cells' nutritional value, as well as on their capacity to oxygenate ocean water.

In order to get further insights on the influence of gene expression in the changes of lipid classes and FAs composition on *P. tricornutum* as a consequence of heat waves, Feijão *et al.* (2020) analysed key genes responsible for the biosynthesis of some lipids, FAs desaturation of plastidial Δ6 desaturase and extraplastidial Δ5 desaturase lipids, as well as phospholipases. The results obtained indicate that storage lipids decrease in response to a heat wave. Besides changing the proportion of membrane/storage lipids, the heat wave also affected the FAs composition of all lipid classes. As a general trend, there is a decrease in PUFA and an increase in saturated or, in some cases, monounsaturated FAs. This could be a mechanism to stabilize the membrane (Feijão *et al.*, 2020). Moreover, Feijão showed that after exposure to heat, the gene encoding the plastidial Δ6 FAs desaturase showed a significant increase. Thus, although no significant change occurred in the Δ5 desaturase transcripts amounts, lower amounts of EPA were detected. Under extreme temperature stress (up to 30°C) *P. tricornutum* hardly shows any growth (Jiang and Gao, 2004) and effects on lipid metabolism are drastic (e.g. no EPA content) (Dodson *et al.*, 2014). This mechanism could involve gene expression regulation of genes related to membrane lipids synthesis e.g. MGDG (with high EPA content). Under non-lethal growth temperatures, *P. tricornutum* could prioritize thylakoid membrane stability and therefore photosynthesis over membrane quality (Feijão *et al.*, 2020).

The marine picocyanobacterium *Synechococcus* is one of the most conspicuous and widely distributed species in the world, with high importance for net primary productivity (Flombaum *et al.*, 2013). Studies of the FAs desaturase-related genes in *Synechococcus* have determined the presence of four main distinct genes, encoding two Δ9- (desC3 and desC4) and two Δ12-desaturases (desA2 and desA3; Varkey *et al.*, 2016). *Synechococcus* has a different physiological strategies based on the presence of specific lipid desaturase gene sets, allowing them to cope with changes in the fluidity of the photosynthetic membrane in different thermal conditions. In a recent latitudinal study, Breton *et al.* (2020) have shown the distribution of such lipid desaturase genes at 33 widespread stations along the Tara Oceans transect. The desaturase gene desC4, which is specific for cold-adapted strains, was found exclusively in waters colder than 20°C, consistent with its hypothesized role of a monodesaturation enhancer enabling growth in cold thermal environments. In warm environments, there is little need to have FAs variations in membrane, and marine *Synechococcus* have adopted a different strategy. They constitutively contain membrane Δ12-lipids with more double unsaturation thanks to DesA2, a desaturase specific to warm environments (30–32°C). Δ9-desaturases were selected in colder environments during the evolution of marine *Synechococcus* as shown in Fig. 1. Thus, after shifting the culture temperature down from 38 to 22°C, Sakamoto *et al.* (1997) demonstrated for *Synechococcus* sp. PCC 7002 strain that the degree of unsaturation of C18 FAs increased in cells grown at low temperature. The desaturation at the ω3 position of C18 increased gradually during a 12-h period in cells grown at 22°C. Various desaturases in cyanobacteria and higher plants are known to be affected by temperature at the level of gene transcription (Los *et al.*, 1997). Wada and Murata (1990) demonstrated that FAs desaturases enzymes play an important role in cold acclimation of cyanobacteria. The microalgal genome contains genes coding for the synthesis of molecules involved in survival mechanisms and FA synthesis (Li *et al.*, 2014). In these organisms, de la Rosa *et al.* (2020) demonstrated a differential sensitivity of ω3 and ω6 FA to high temperature. They observed decreased relative concentration of 18:4ω3 and 18:3ω3 at 29°C after 10-days exposure as compared to exposure to 26°C. Previous studies also have shown an effect of temperature on the FA composition, and specifically a decrease in ω3 PUFA (EPA and DHA) with increasing temperature. Thus, Sushchik *et al.* (2003) demonstrated a decrease of ω3 FA desaturase due to increased temperature in *Chlorella vulgaris* and *Botryococcus braunii* resulted in a decrease in the relative content of the more unsaturated intracellular FAs, especially the trienoic FAs like ALA. Also, for *Thalassiosira pseudonana*, the percentage of 22:6w3 decreased linearly with increasing temperature over the range from 10 to 25°C (Thompson *et al.*, 1992).

Hence, the adaptation of *M. aeruginosa* to temperature rise could be related to a decrease and an increase in the activity of ω3 and ω6-desaturases, respectively. The high relative abundance of cis-18:1ω9, observed in high temperature conditions from day 1 of incubation and until the end of the 10-days experiment (de la Rosa *et al.*, 2020), could explain the significant increase of the PUFA ω6, considering that this MUFAs cis-18:1ω9 is a precursor of the ω6 FAs (Akoh and Min, 2008).

Conclusions

FAs in phytoplankton and cyanobacteria display structural changes and high biological specificity, responding to stress conditions. Their biosynthesis is inhibited or enhanced depending on the temperature the organisms are exposed to, along with alterations in the processes of FAs desaturation and elongations. Hence, FAs are useful bioindicators of the ecological and health status of aquatic ecosystems. They provide crucial information about the impact of global stressors on aquatic communities and thus on the food web, with severe repercussions to human beings among other terrestrial animals, and food quality. Moreover, lipids and proteins are involved in the most vital functions of aquatic organisms. Thus, the reduction of essential FAs content at the base of the food web may have serious implications for higher trophic levels.

As consequences of climate change effects on marine and freshwater ecosystems, intensive agriculture production with the usage of fertilizers and pesticides near coastal wetlands will have severe impacts on the aquatic communities and thus to whole the ecosystem. Therefore, it is of major importance and becomes a priority to determine and predict the effects of environmental and anthropogenic stressors on the aquatic systems in order to promote their health and preserve biodiversity and food quality.

Overall, heat wave-induced changes in the relative abundance of PUFA, and more importantly EPA, are alarming because of their importance in aquatic ecosystems. However, the impact of the exposure of aquatic communities to climate change variables is different between temperate/tropical and polar environments. In cold marine waters the activation of desaturase is promoted towards high-energy ω3 FAs such as EPA. Conversely, in temperate and tropical environments, the decrease in EPA as a function of desaturases sensitivity protects the photosystems in conditions of high irradiance and heat waves.

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