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Climate warming is predicted to reduce omega-3, long-chain, polyunsaturated fatty acid production in phytoplankton

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Abstract

Phytoplankton are the main source of energy and omega-3 (n-3) long-chain essential fatty acids (EFA) in aquatic ecosystems. Their growth and biochemical composition are affected by surrounding environmental conditions, including temperature, which continues to increase as a result of climate warming. Increasing water temperatures may negatively impact the production of EFA by phytoplankton through the process of homeoviscous adaptation. To investigate this, we conducted an exploratory data synthesis with 952 fatty acid (FA) profiles from six major groups of marine and freshwater phytoplankton. Temperature was strongly correlated with a decrease in the proportion of n-3 long-chain polyunsaturated FA (LC-PUFA) and an increase in omega-6 FA and saturated FA. Based on linear regression models, we predict that global n-3 LC-PUFA production will be reduced by 8.2% for eicosapentaenoic acid (EPA) and 27.8% for docosahexaenoic acid (DHA) with an increase in water temperature of 2.5 °C. Using a previously published estimate of the global production of EPA by diatoms, which contribute to most of the world's supply of EPA, we predict a loss of 14.2 Mt of EPA annually as a result of ocean warming. The n-3 LC-PUFA are vitally important for an array of key physiological functions in aquatic and terrestrial organisms, and these FA are mainly produced by phytoplankton. Therefore, reduced production of these EFA, as a consequence of climate warming, is predicted to negatively affect species that depend on these compounds for optimum physiological function. Such profound changes in the biochemical composition of phytoplankton cell membranes can lead to cascading effects throughout the world's ecosystems.

Keywords: climate change, docosahexaenoic acid, eicosapentaenoic acid, global warming, omega-3 long-chain polyunsaturated fatty acids

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Introduction

Phytoplankton account for nearly half of net primary production on earth and produce many complex biomolecules (Field *et al*., 1998), including lipids and fatty acids (FA) (Guschina & Harwood, 2009). Lipids produced by phytoplankton provide energy and essential nutrients for consumers in aquatic (Guschina & Harwood, 2009; Parrish, 2013) and terrestrial ecosystems (Gladyshev *et al*., 2009; Hixson *et al*., 2015). In addition to their nutritive role, lipids form the backbone of the lipid bilayer in cell membranes. The precise composition of cell membrane lipids is critical for the structure and function of all organisms and is thus considered to be an important driver of organismal and ecosystem health and stability (Arts *et al*., 2009; Parrish, 2013).

Long-chain (i.e., ≥20 carbons) polyunsaturated fatty acids (LC-PUFA) are bioactive compounds that are critically involved with key physiological functions in all animals, including humans. They have been shown to support neurological function, cardiovascular health, vision, growth, reproduction, and the immune response (Arts *et al*., 2001; Arts & Kohler, 2009; Brenna *et al*., 2009; Simopoulos, 2011; Parrish, 2013; Calder, 2015). Two omega-3 (n-3) LC-PUFA that are known to have distinctly important functions include eicosapentaenoic acid (EPA; 20:5n-3) and docosahexaenoic acid (DHA; 22:6n-3). These LC-PUFA are produced from their precursor, alpha-linolenic acid (ALA; 18:3n-3), which is considered an essential fatty acid (EFA) as vertebrates lack the enzymes necessary to form ALA (Cook & McMaster, 2004). However, the direct physiological function of ALA in organisms is limited, as its main purpose is as an energy source or as a precursor to the physiologically important EPA and DHA (Tocher, 2003). While consumption of ALA is required for all vertebrates, consuming preformed EPA and DHA is highly advantageous for vertebrates, because most have a limited ability to synthesize LC-PUFA (Parrish, 2009), including humans (Cook & McMaster, 2004).

The n-3 LC-PUFA are mainly synthesized by phytoplankton in aquatic food webs and are generally not

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synthesized, to any great degree, by primary producers or many primary consumers in terrestrial ecosystems (Hixson *et al*., 2015; Twining *et al*., 2015). These LC-PUFA are produced in relatively large amounts by some phytoplankton (e.g., diatoms, cryptophytes, dinoflagellates; Brett & Müller-Navarra, 1997), as well as macrophytes (Galloway *et al*., 2012), and 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 the terrestrial ecosystem via consumption (Gladyshev *et al*., 2009, 2013). The LC-PUFA composition of 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).

Climate modelers predict that both surface air temperatures and the frequency of extreme heat days will continue to increase (IPCC, 2014). Driven by these two phenomena, marine and freshwater temperatures will also continue to rise (IPCC, 2014). Aquatic ecosystems with large surface-to-volume ratios are particularly vulnerable (i.e., small ponds and large shallow lakes; McKee *et al*., 2002; Van Doorslaer *et al*., 2007). Because phytoplankton growth and composition are highly dependent on environmental conditions (Guschina & Harwood, 2009; Galloway & Winder, 2015), and because organisms on this planet depend on the resources that phytoplankton supply, there is an urgent need to understand how life will be affected, at the biochemical level, in our warming world.

Temperature is expected to have strong directional effects on the quantity and quality of FA in phytoplankton. Phytoplankton and other organisms adapt to changing temperatures by modifying the structure of their membranes (Winter & Dzwolak, 2005; D'Amico *et al*., 2006), a process known as homeoviscous adaptation (Sinensky, 1974). This adaptation involves remodeling membrane lipids by modifying FA chain length and unsaturation to maintain a desired level of fluidity in cell membranes (Sinensky, 1974; Guschina & Harwood, 2006). The double bonds in PUFA enhance the ability of FA to 'bend' and increase flexibility, leading to increased membrane fluidity. Thus, phytoplankton are expected to increase membrane PUFA content in response to decreasing temperatures in order to maintain fluidity (Ackman & Tocher, 1968; Thompson *et al*., 1992; Renaud *et al*., 2002; Guschina & Harwood, 2006). Conversely, acclimation to increasing temperature involves decreasing PUFA membrane content, while, simultaneously, increasing saturated fatty acids (SFA), to maintain cell membrane structural rigidity in a less ordered environment (Rousch *et al*., 2003; Fuschino *et al*., 2011).

An important, and as yet not fully appreciated, threat posed by climate change is that increasing water temperatures are expected to reduce the global production of PUFA in phytoplankton. Such changes in the biochemical composition of phytoplankton cell membranes may lead to cascading effects throughout the world's aquatic ecosystems. Further, the repercussions of these biochemical and physiological cascades are also anticipated to propagate to terrestrial animals because of the flux of aquatic biomass, containing n-3 LC-PUFA, which routinely passes from aquatic to terrestrial ecosystems (Gladyshev *et al*., 2009, 2013). This is critical because LC-PUFA not only enhance the growth rates and reproductive capacities of aquatic animals (Ballantyne *et al*., 2003; von Elert, 2004), but are also vitally important to the neural/cognitive, cardiovascular, and visual health of terrestrial vertebrates (Lands, 2009; Calder, 2015).

While isolated individual studies have shown that phytoplankton increase their PUFA content in response to colder temperature, the effect of warming temperatures on PUFA content (especially n-3 LC-PUFA) has not yet been confirmed in a systemic way and on a global scale. Therefore, the objective of our data synthesis was to estimate the effect that increasing water temperatures will have on n-3 LC-PUFA composition and production in phytoplankton.

Materials and methods

Data collection

FA data from freshwater and marine phytoplankton were collected from the primary, peer-reviewed, scientific literature. Articles were retrieved through the following databases: Google Scholar©, Scholars Portal©, and Web of Science©. The following search terms were used: algae, cyanobacteria, FA, lipid, phytoplankton, PUFA, temperature. In addition to this, certain FA profiles (from proportional data) and the associated temperature from the data set created by Galloway & Winder (2015) were used, and the FA of interest (listed below) were selected from each profile. Unpublished FA data (n = 5) from M.T. Arts were also used. The data were sorted into six major phytoplankton taxa (referred to as 'groups' from here on): Chlorophyta, Cryptophyta, Cyanobacteria, Diatoms (which included Bacillariophyceae, Coscinodiscophyceae, and Fragilariophyceae), Dinophyta, and Haptophyta. The data were also sorted by geographic origin and were characterized by four regions, which were latitudinally defined: polar (90–60°N and S), temperate (60–30°N and S), tropical (30°N to 30°S), or cosmopolitan (occupies two or more regions). We noted the geographic origin for each data point as listed in the original primary article, if possible, in both cases where samples were obtained from the wild and when laboratory cultures were obtained a natural source. In cases where cultures were obtained from a collection, we used Algaebase (http://

www.algaebase.org/) and/or the World Register of Marine Species (WoRMS; http://www.marinespecies.org/index.php) to obtain information on environment and global distribution.

To qualify for inclusion in the data set, the data were required to be species specific and present all FA of interest: ALA, linoleic acid (LNA; 18:2n-6), EPA, DHA, arachidonic acid (ARA; 20:4n-6) as well as the sums of SFA, monounsaturated FA (MUFA), and PUFA (or total FA along with a complete list of FA to calculate these sums). The FA data must have been presented as relative FA %. Although it would have been preferable to perform a data synthesis on FA contents expressed as mass fractions (mg g^{-1}), the majority of studies present FA data on a proportional basis (i.e., %); therefore, using proportional data increased the number of FA profiles available for us to include in the data synthesis. Although reported values of proportional FA data depend on the total number of identified FA, our main objective was to investigate differences in FA patterns as a result of temperature and species, and as such, analytical differences among the investigated studies were considered of minor importance. FA data were excluded when presented on a weight per weight (w/w) basis or a weight per volume (w/v) basis due to the inability to accurately convert these quantitative measurements to the desired format. The growth or collection temperature must have been accompanied by the associated FA profile(s). Outliers were managed by reviewing the data compiled for each FA within taxa, and a Grubb's outlier test was conducted to determine significant outliers ($P < 0.05$). If a significant outlier was detected, the original source of the information was reviewed, and if an error was perceived, that data entry was removed from the data set.

Relationships with temperature analyses

Linear regression analyses were conducted to relate phytoplankton FA with growth temperature, with each individual FA as the dependent variable and temperature as the independent variable. In specific cases, a segmented nonlinear regression was performed. In these cases, it was apparent that for different temperature ranges, more than one linear relationship was present, and so a single linear model may not provide an adequate description of the data. The temperature (on the x-axis) where the fitted functions intersect is defined as the break point (Ryan & Porth, 2007) and represents a critical temperature where the relationship between FA level and temperature changes. The value of the break point is estimated in the analysis. When there is only one break point at $x = T$, the model is written as follows: $y = a_1 + b_1x < T$; $y = a_2 + b_2x > T$. The least squares method is applied to each segment, by which the two regression lines are made to fit the data set as closely as possible while minimizing the sum of square differences between the observed and calculated values of the dependent variable (PUFA level), which results in two linear equations (Ryan & Porth, 2007). If a segmented nonlinear regression was significant, then two separate regressions were conducted before and after T (the break point on the x-axis which segments the original linear regression). The significance of the break point is indicated by the 95% confidence area around the point at x. We report the r^2 values, as well as the significant break points in the relationship (T, $P < 0.05$). Pearson correlations were conducted at the genus level for each phytoplankton group to indicate the significance and directionality of the relationship between FA and temperature. Regression and correlation analyses were conducted in SIGMAPLOT 11.0 (Systat Software, Inc., San Jose, CA, USA).

Similarity in percentage analysis

Similarity in percentage (SIMPER) analysis was used to differentiate phytoplankton FA profiles based on temperature as a categorical variable (as in Xue *et al.*, 2014, 2015). Temperature data associated with each FA profile was divided into four quartiles (low, medium–low, medium–high, and high) that were statistically defined in Minitab (Minitab 16 Statistical Software). Each quartile represented a temperature range (see Table S3 for exact temperature range for quartiles in each group). Each FA profile was assigned the appropriate temperature quartile based on the temperature associated with that FA profile. The similarity coefficient in SIMPER is defined to take values in the range (0–100%) with the ends of the range representing the extreme possibilities: $S = 100\%$ if two samples are totally similar and $S = 0\%$ if two samples are totally dissimilar. The nonmetric Bray–Curtis dissimilarity statistic was used to quantify the compositional dissimilarity between samples (Bray & Curtis, 1957). This measure delivers robust and reliable dissimilarity results and is one of the most commonly applied measurements to express relationships in ecology, environmental sciences, and related fields (Clarke & Warwick, 2001). SIMPER analyses were conducted in PRIMER (Plymouth Routines in Multivariate Ecological Research; PRIMER-E Ltd., version 6.1.15, Plymouth, UK).

Analysis of variance

A series of analysis of variance (ANOVA) and analysis of covariance (ANCOVA) models were used to determine whether taxonomy, geographic origin, and/or temperature have a significant effect on FA composition in phytoplankton. Taxonomy (fixed factor) included 6 groups (chlorophytes, cryptophytes, cyanobacteria, diatoms, dinophytes, and haptophytes). Temperature (random factor) used the same 4 temperature quartiles that were used in the SIMPER analysis (low, medium–low, medium–high, and high). Geographic origin (random factor) was characterized by four regions, which were latitudinally defined: polar (90–60°N and S), temperate (60–30°N and S), tropical (30°N to 30°S), or cosmopolitan (occupies two or more regions).

First, a three-way ANOVA was used to test the effects of major taxonomic group (six groups), geographic origin (four levels, listed above), and temperature (four levels, listed above) on FA composition in phytoplankton. The interaction between taxonomy and geographic origin was tested. This model included all FA profiles in the data set ($n = 952$).

Second, another series of three-way ANOVAs were used to test the effect of taxonomy, geographic origin, and temperature on FA composition within each of the six major groups. In this set of three-way ANOVAs (six total, one for each major taxonomic group), class within each group was tested as the

taxonomy factor (the number of classes varied depended on the data collected for that major group). The interaction between taxonomy and geographic origin was not tested in this model because the design was unbalanced, as not all classes were represented in each geographic region.

Third, an ANCOVA model was used to determine whether taxonomy and/or geographic origin (categorical variables) explained the variation in the segmented linear regression models (temperature as the covariate), both before and after the break point (≤16 °C and ≥16 °C) for the whole group data set (EPA and DHA only).

Differences were considered significant at $P < 0.05$. The ANOVA/ANCOVA models were conducted in Minitab (Minitab 16 Statistical Software).

Estimated declines in phytoplankton PUFA

Predictive estimates for the production of EPA and DHA by phytoplankton were based on regression slopes and calculated based on increases in water temperature of 2.5 °C (from 20 °C to 22.5 °C). The mean temperature of all FA profiles in the data set ($n = 952$) was 19.8 °C; therefore, we started our base calculation at 20 °C. We estimated increases in water temperature according to the IPCC climate scenarios A2, which predicted an increase in surface air temperature between 1.3 and 4.5 °C up to year 2100 (Houghton *et al.*, 2001), and that was used in a simulated global warming mesocosm (Van Doorslaer *et al.*, 2007), which modeled scenarios at 19.6 °C, 23.4 °C, and 25.4 °C based on the same climate warming scenario (Houghton *et al.*, 2001). Calculation of global production of EPA by diatoms used the estimate provided by Budge *et al.* (2014) combined with our estimate in reduction based on a putative global warming scenario. For this calculation, we estimated an increase in water temperature of 2.5 °C (from 20.5 °C to 22.5 °C). We used the slope of the line calculated from the regression of EPA with temperature in the diatom group to calculate the decrease in EPA production based on the defined temperature increase and the estimate by Budge *et al.* (2014).

Results

Fatty acid profiles

A total of 952 FA profiles from marine and freshwater phytoplankton were amassed from primary literature, along with the associated growth/collection temperature (Tables S5–S10). Many of the references in the present data set were also used in the Galloway & Winder (2015) data set. The database was divided into 6 taxonomic groups: diatoms ($n = 332$), chlorophytes ($n = 242$), haptophytes ($n = 137$), cyanobacteria ($n = 98$), cryptophytes ($n = 93$), and dinophytes ($n = 50$). The phytoplankton included in the data synthesis were geographically distributed, with phytoplankton represented in temperate ($n = 263$), polar ($n = 225$), and tropical ($n = 99$) regions, with most phytoplankton inhabiting more than one region, and were defined as cosmopolitan ($n = 358$).

Relationships between phytoplankton FA composition and temperature

Results describe significant relationships only ($P < 0.05$); however, all results are shown in Table 1, Figs 1–3, and Tables S1–S4.

All groups

When all groups were included, EPA, DHA, and total SFA decreased with increasing temperature (Table 1; Table S1). LNA and ARA increased with increasing temperature. For EPA and DHA, there appeared to be different linear relationships for different temperature ranges, so a single linear model may not have provided the best fit for the data. Therefore, a two-segmented nonlinear regression model was applied to the relationship between temperature and EPA and DHA. A significant break point was observed at 16 °C in both the EPA and DHA vs. temperature plots (Fig. 1). Two linear regression models, for EPA and DHA separately, were applied (before and after the break point). For EPA, the linear relationship with temperature before the break point ($x < 16$ °C) was not significant; however, after the break point, EPA significantly decreased after the temperature was >16 °C ($P = 0.001$; $r^2 = 12.5$; [EPA = 14.1−(0.279) × °C]). For each linear model

Table 1 Linear regression slopes for the relationship between water temperature and fatty acid composition in various groups of phytoplankton*

Phytoplankton group	LNA	ALA	ARA	EPA	DHA	PUFA	MUFA	SFA
All groups	**0.251**	0.058	**0.059**	**−0.157**	**−0.064**	−0.098	−0.145	**−0.181**
Diatoms	0.019	0.003	**0.138**	**−0.326**	**−0.058**	**−0.433**	−0.095	**0.271**
Chlorophytes	**0.131**	**−0.255**	NA	NA	NA	−0.269	0.033	**−0.607**
Cryptophytes	−0.077	0.190	0.009	**−0.260**	**−0.078**	**−0.542**	−0.100	**0.475**
Dinophytes	3.71	0.006	**0.060**	**0.476**	**−0.807**	0.627	−0.278	−0.402
Haptophytes	0.055	**0.119**	**0.008**	**0.301**	0.088	**0.873**	**−0.275**	**−0.517**
Cyanobacteria	**0.379**	−0.164	NA	NA	NA	0.256	0.261	−0.267

*Slopes in bold indicate a significant relationship, $P < 0.05$.

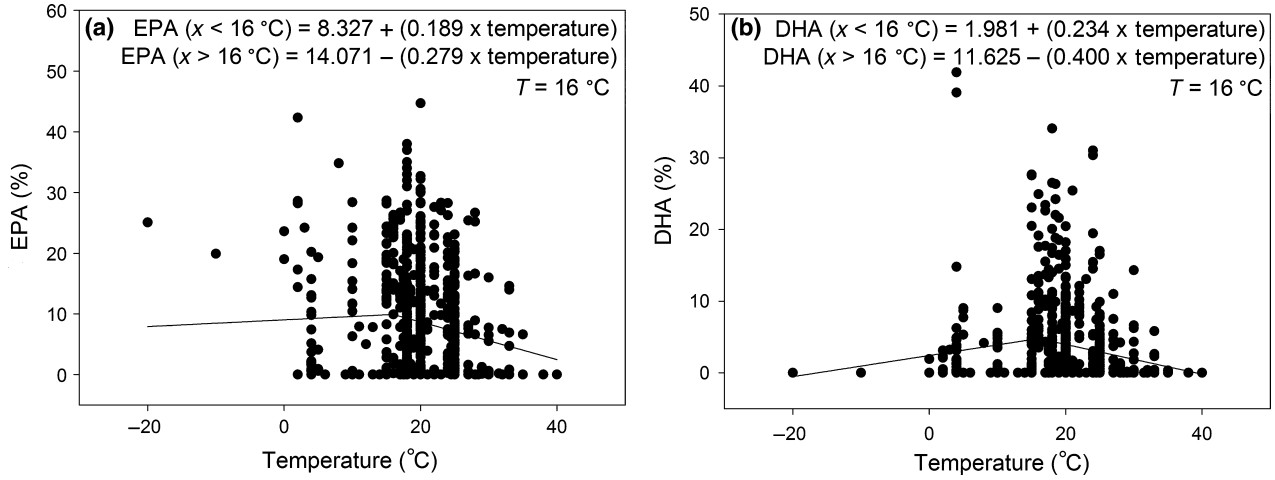

Fig. 1 Two-segmented nonlinear regression with (a) EPA and (b) DHA and temperature in all phytoplankton groups. For both EPA and DHA, the break point is T = 16 °C.

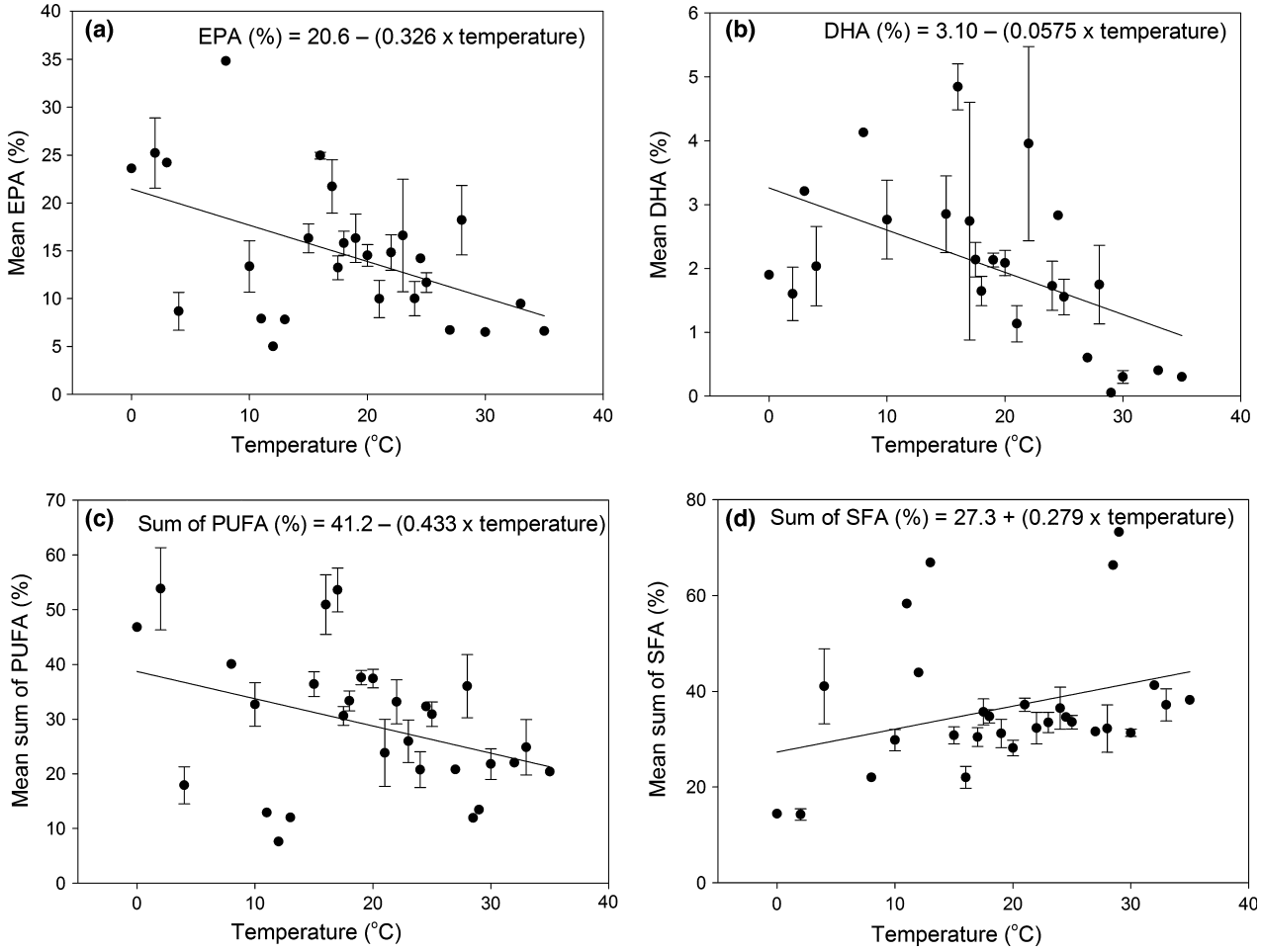

Fig. 2 Linear regressions showing the relationship between temperature and diatom fatty acids (mean ± standard error): (a) EPA, (b) DHA, (c) sum of PUFA, and (d) sum of SFA (P < 0.01).

before and after the break point, both taxonomy and geographic origin (P < 0.001) were significant factors. At temperatures up to 16 °C, DHA significantly increases (P = 0.010; r^2 = 16.9%; [DHA = 1.98 + (0.234 × °C)]. At temperatures greater than 16 °C, DHA significantly decreases (P = 0.043; r^2 = 9.2%;

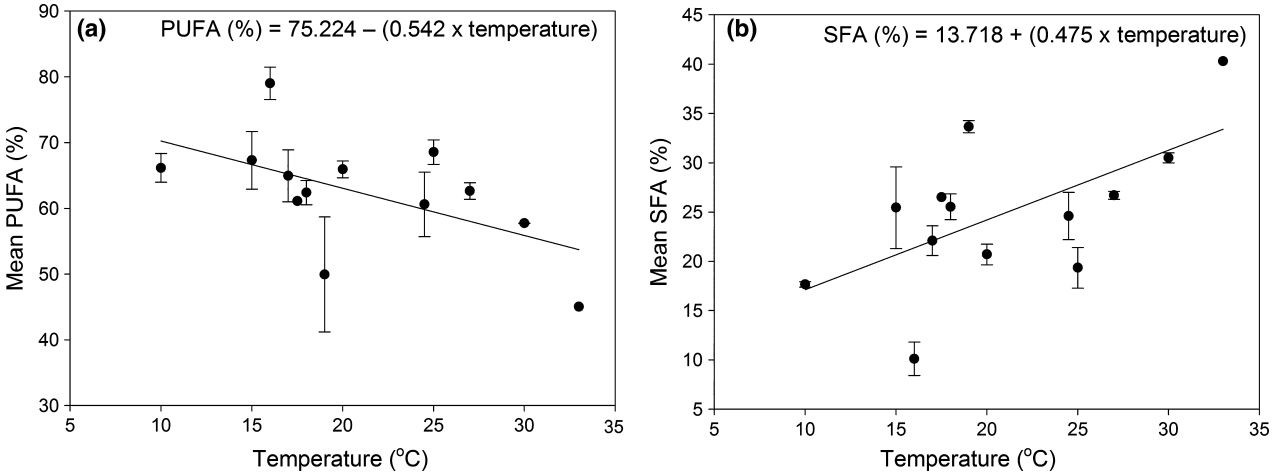

Fig. 3 Linear regressions showing the relationship between temperature and cryptophyte fatty acids (mean ± standard error): (a) PUFA and (b) SFA. ($P < 0.05$).

[DHA = 11.6 − (0.40 × °C)]. Taxonomy was a signifi cant factor before and after the break point ($P < 0.001$), but geographic origin was not before ($P = 0.251$) and after ($P = 0.367$) the break point.

Group level

In diatoms, the linear regression models with EPA, DHA, and PUFA showed a negative linear relationship with temperature (Table 1; Fig. 2; Table S1). Conversely, ARA and SFA increased with temperature. In chlorophytes, ALA and SFA decreased with temperature, while LNA increased with temperature. In cryptophytes, EPA, DHA, and total PUFA decreased with increasing temperature, while total SFA increased with temperature (Fig. 3). In dinophytes, ARA and EPA increased with temperature, while DHA decreased with temperature. In haptophytes, ALA, ARA, EPA, and total PUFA increased with temperature, while total MUFA and total SFA decreased with temperature. In cyanobacteria, LNA increased with temperature.

Genus level

For diatoms, in the genera *Nitzchia* and *Odontella*, EPA and PUFA were negatively correlated with temperature (Table S2). *Chaetoceros*, *Odontella*, and *Phaodactylum* showed positive correlations with ARA and temperature. *Odontella* showed negative correlations with both LNA and ALA and temperature, and positive correlation with total SFA. For chlorophytes, *Chlamydomonas* showed a negative correlation with ALA and temperature. *Chlorella*, *Nanochloris*, and *Stichococcus* showed positive correlations between LNA and temperature, while *Chlamydomonas* showed a negative correlation. *Botrycoccus* showed a negative correlation between PUFA and temperature, but positive correlation with MUFA. *Chlorella* and *Stichococcus* showed negative correlations between total SFA and temperature. *Chlamydomonas* showed a negative correlation between MUFA and temperature. In cryptophytes, *Rhodomonas* showed a negative correlation with both EPA and DHA and temperature, and a positive correlation with SFA and temperature. In dinophytes, *Amphidinium* showed a positive correlation between ARA and temperature. *Gymnodinium* showed negative correlations in both MUFA and SFA with temperature, and a positive correlation between PUFA and temperature. In haptophytes, *Isochrysis* showed a positive correlation between ALA and temperature.

Similarity in percentage analysis

The SIMPER analysis determined differences in FA composition based on temperature ranges (Table S3). The FA profiles of diatoms, chlorophytes, and haptophytes, grown in high temperatures (T4) vs. low temperatures (T1), were the most dissimilar (ranging from 27.5 to 32.6% different). In cryptophytes, FA profiles from T3 and T1 were most dissimilar (22.5%). In dinophytes, FA profiles from T3 and T4 were most dissimilar (46.9%). In cyanobacteria, T2 and T4 were most dissimilar (52.0%). PUFA was the major contributing FA group to the dissimilarities in each comparison.

Analysis of variance

When all phytoplankton groups were analyzed together, taxonomy (on a group basis), geographic origin, and temperature were all significant factors in

determining the proportion of most of the FA, as well as the interaction between taxonomy and geographic origin (Table S4).

When the model was run for each group separately, we found that, in diatoms, temperature was a factor for all FA, as well as geographic origin (except LNA), while taxonomy was a significant factor for EPA and total PUFA. For chlorophytes, temperature was a factor for LNA, ALA, MUFA, and SFA, geographic origin was a factor for PUFA and SFA, while taxonomy (on a class basis) was not a significant factor. For cryptophytes, temperature was a factor for all FA (except ALA), geographic origin was a factor for LNA, ARA, DHA, and MUFA, while taxonomy (on a class basis) was also a factor in EPA and DHA. For haptophytes, temperature was a factor for all FA, geographic origin was a factor for all FA (except SFA), while taxonomy (on a class basis) was a factor for LNA, ALA, EPA, and total MUFA. In cyanobacteria, temperature was a factor for LNA and PUFA, geographic origin was a factor for PUFA, MUFA, and SFA, but taxonomy (on a class basis) was not a significant factor for any FA. In dinophytes, temperature was a factor for ARA, EPA, and DHA content, geographic origin was a factor for ALA, ARA, EPA, and DHA, but taxonomy (on a class basis) was not a factor.

Future declines in phytoplankton PUFA

Estimates of the potential reduction in PUFA content can be approximated based on the calculated change in FA content (using the slope from linear regression models; Table 1) due to a prescribed increase in water temperature. For all phytoplankton groups combined, based on the linear segmented model (i.e., >16 °C), an increase in temperature from 20 to 22.5 °C could result in an 8.2 and 27.8% reduction in EPA and DHA, respectively.

Similarly, an increase in water temperature from 20 to 22.5 °C could result in a 5.9 and 7.4% reduction in EPA and DHA (respectively) in diatoms, and a 7.6 and 9.7% reduction in EPA and DHA (respectively) in cryptophytes. In chlorophytes, we estimated a 3.2% reduction in ALA content with an increase in water temperature from 20 to 22.5 °C.

Using the estimate by Budge *et al.* (2014), we can predict how increasing temperature due to global warming will affect the amount of EPA produced by diatoms globally. The reduction in EPA in diatoms due to a 2.5 °C increase (i.e., 20 to 22.5 °C) is 5.9%. The current estimate for global EPA production by diatoms is 240 Mt yr^{-1}. Therefore, a reduction of 5.9% would represent a 14.2 Mt loss of EPA on a yearly basis on a global scale.

Discussion

Previous studies with individual phytoplankton species have shown that temperature affects FA composition and that n-3 PUFA content generally decreases with increasing temperature (Ackman & Tocher, 1968; Thompson *et al.*, 1992; Renaud *et al.*, 2002; Guschina & Harwood, 2006). However, our data synthesis is the first time that such information has been compiled on a large scale and specifically related to the effects of global warming. Our analysis, which included 952 phytoplankton FA profiles, revealed several clear relationships between phytoplankton FA composition and increasing water temperature. These relationships support the idea that phytoplankton modify their cell membrane FA composition in order to adapt to changes in ambient temperature (i.e., homeoviscous adaptation). Generally, n-3 LC-PUFA (EPA and DHA) decreased with increasing temperature, while n-6 PUFA (LNA and ARA), as well as SFA, tended to increase with rising temperatures.

Our data synthesis represented 6 major phytoplankton taxa. We note that, while our search was thorough, our selection criteria may have imposed a bias on the groups/genera/species of phytoplankton that were included. For example, the FA profiles of certain phytoplankton groups (diatoms and chlorophytes) were better represented in the literature than others (cryptophytes, dinophytes, and haptophytes). Grouping species together also introduced a degree of variability, as phylogeny is a known driver of FA composition (Budge *et al.*, 2002; Dalsgaard *et al.*, 2003; Galloway & Winder, 2015); therefore, different genera within a major phytoplankton group may naturally have different FA composition, regardless of environmental conditions (Galloway & Winder, 2015). Also, variation within groups is expected given that our data set came from studies that used a variety of different culture methods and were premised on a range of different study objectives, as similarly described in Galloway & Winder (2015). Despite this variation and potential bias, the major, globally significant, phytoplankton PUFA producers were well represented. Further, our analysis showed that the effect of lower level taxonomy (i.e., within phyla) was minimal compared with the effect of temperature. The key conclusion, based on our data synthesis, is that increasing water temperatures, as a result of global warming, is predicted to result in major shifts in phytoplankton PUFA production.

We found strong overarching responsive relationships between FA and temperature in at least 6 major groups of phytoplankton, with both the degree of unsaturation and FA type (n-3 or n-6) emerging as key

factors that determine FA composition as a function of temperature. Our results agree with previous studies on individual species that quantified decreases in phytoplankton PUFA as the temperature increases (Rousch *et al.*, 2003; Fuschino *et al.*, 2011; Pasquet *et al.*, 2014). At cold temperatures, upregulation of gene expression for desaturases in phytoplankton is likely to be a major factor in increasing production of PUFA (Guschina & Harwood, 2006). The effect of oxygen on the activity of desaturases is also notable because oxygen solubility increases at lower temperatures; therefore, lower temperatures and higher oxygen levels may induce desaturase activity, resulting in higher levels of unsaturated FA (Guschina & Harwood, 2006). The opposite scenario is plausible at higher temperatures with lower oxygen availability, resulting in a decrease in desaturase activity. Further, our analysis revealed that increased temperatures were generally negatively correlated with n-3 PUFA and positively correlated with n-6 PUFA. This opposing relationship between n-3 and n-6 PUFA is plausible from a biosynthesis perspective. This is because synthesis of the n-3 and n-6 LC-PUFA depends on the activities of the same enzymes (desaturases and elongases) such that competition for enzymes, in the context of increasing ambient water temperatures and reduced oxygen levels, tends to favor n-6 over n-3 production. An increase in production of n-6 over n-3 LC-PUFA could negatively impact vertebrates, as the n-6 (ARA) is a precursor to inflammatory eicosanoids, while the n-3 (EPA) is a precursor to anti-inflammatory eicosanoids (Arts & Kohler, 2009); therefore, an imbalance in this ratio can be detrimental to the immune response and cardiovascular health of vertebrates.

At the group level, the relationship between SFA and temperature is more variable than the strong pattern observed with n-3 LC-PUFA. Homeoviscous adaptation suggests that a decrease in PUFA production would balance with an increase in production of SFA; however, for some genera, a decrease in SFA is observed. In these cases, we observed an increase in MUFA rather than SFA. MUFA may also increase in phytoplankton cell membranes in response to temperature under certain conditions (Fuschino *et al.*, 2011; Piepho *et al.*, 2012). This could depend on the FA composition during the time of temperature adaptation, which is subject to nutrient availability and other environmental conditions, as well as species.

It is well known that phylogeny is a driver of FA composition in a wide range of organisms (Budge *et al.*, 2002; Dalsgaard *et al.*, 2003; Galloway & Winder, 2015). Environmental conditions clearly affect phytoplankton FA profiles, but these conditions often account for relatively low variation compared with phylogeny (Galloway & Winder, 2015). To assess this hypothesis, we tested taxonomy and temperature as factors affecting FA composition in phytoplankton, on both the group and class levels. Considering all six major groups combined, it was clear that both taxonomy and temperature were influencing phytoplankton FA composition. However, when the model was run with each group separately, taxonomic class was not as prominent as temperature with respect to determining phytoplankton FA composition. Therefore, the effect of temperature is emphasized when comparing phytoplankton of the same taxonomic class that naturally have similar FA compositions. For example, in an ecosystem that is consistently dominated by diatoms, increases in temperature will significantly reduce production of n-3 LC-PUFA. More importantly, we found that the world's major PUFA producers of (diatoms, chlorophytes, cryptophytes, and dinophytes) demonstrate an overall reduction in n-3 LC-PUFA in response to increasing temperatures. Temperature also influences the composition of phytoplankton species present, which can alter the types of FA produced (Galloway & Winder, 2015). For example, increased water temperature favors the growth of harmful algal blooms (i.e., cyanobacteria; Paerl & Paul, 2012). This effectively reduces n-3 LC-PUFA production because cyanobacteria compete with and dominate other phytoplankton species (which may be significantly contributing to n-3 LC-PUFA production; Paerl & Paul, 2012), and because cyanobacteria do not produce EPA or DHA (Caramujo *et al.*, 2008). This suggests that climate change may reduce n-3 LC-PUFA as a direct influence of temperature on altering production by phytoplankton, as well as by altering species composition to favor groups that do not produce n-3 LC-PUFA.

Geographic origin, latitudinally defined as polar, temperate, tropical, or cosmopolitan, also influenced FA composition. Considering all major phytoplankton groups combined, geographic origin and taxonomy were interacting factors that determined FA composition. As temperature is intrinsically related to latitude, it is not surprising that phytoplankton location was a factor in explaining FA composition. This also explains some of the variability in our models, as phytoplankton inhabiting regions of different latitudes adapt to different range of temperatures, and tolerance to high temperatures may define the biogeographical boundaries of phytoplankton (Teoh *et al.*, 2013). Cold-adapted (i.e., polar) phytoplankton naturally have lower optimal growth temperatures than phytoplankton adapted to thrive in warm tropical regions. However, even after accounting for these latitudinal differences, temperature remained a significant driver of phytoplankton PUFA content in our models. Further, rising temperatures as a result of climate change may alter

phytoplankton composition; competition between species may restrict their distribution to certain regions (Teoh *et al*., 2013), resulting in species that are tolerant of higher temperatures and produce different proportions of LC-PUFA, which reflects the importance of both phylogeny and geographic origin (and their interaction) in the future production of LC-PUFA.

Temperature used as a predictor in the linear regression models with FA yielded not only the nature of the relationship (i.e., positive or negative), but also the degree in which phytoplankton modify certain FA in response to temperature change. Although the r-squared values for the observed linear relationships were low ($r^2 < 16\%$), this is of lesser importance in comparison with the direction (and value) of the slope and general patterns among FA. We expected high variability in the linear models in such a diverse data set due to the fact that different species have different FA profiles, different growth conditions existed in the source studies, and species have different optimal temperatures, etc. We attempted to reduce some of the variability in FA content at a single point on the x-axis by accounting for the optimal temperature for each genus in the model. However, the optimal growth temperature of a given phytoplankton species is not frequently provided; therefore, only a subset of studies in our data set included optimal temperatures which significantly reduced the size of our data set. Further, most of the genera included in the data set can grow in a wide range of temperatures and environmental conditions. As a result, attempting to account for optimal temperature was, at best, an imperfect exercise and did not improve the variability (r^2 values) in our linear models.

To better capture the effects of temperature, we used SIMPER to distinguish differences in phytoplankton FA profiles in four temperature ranges (low, medium–low, medium–high, and high). This analysis provided a broader view of the overall patterns observed in the linear models. Diatoms, cryptophytes, and chlorophytes grown at high or medium–high temperatures showed markedly different FA content than those grown at low temperatures, and the PUFA content was the factor responsible for the most dissimilarity between the high- and low-temperature groups. This confirms that FA content is modified as a result of temperature change, with the two extreme temperatures (cold and warm) driving the difference in FA content. Again, this was due primarily to the fact that certain FA (i.e., EPA and DHA vs. LNA and/or individual SFA) or FA groups (i.e., PUFA vs. SFA) are either increased or reduced in cell membranes in order to allow phytoplankton to adjust (homeoviscous adaptation) cell membrane fluidity in response to temperature change.

The linear regression model for EPA and DHA for all phytoplankton groups combined showed a significant reduction with increasing water temperature. However, the model appeared to split roughly midway along the *x*-axis, suggesting two distinct linear models, which we confirmed using break point analyses. This critical break point value has important implications for EPA and DHA production. At temperatures over 16 °C, significantly less EPA and DHA will be produced with every degree increase in temperature. Interestingly, Galloway & Winder (2015) noted a similar hump-shaped relationship between temperature and, in their case, the sum of EPA + ARA + DHA in phytoplankton, with the highest content of the sum of these LC-PUFA occurring at ~25 °C. We suggest that enzymatic activity of desaturases increases with increasing water temperature (above 0 °C), resulting in greater n-3 LC-PUFA synthesis. However, once the optimum temperature is reached (e.g., ~16 °C as our model indicates), enzymatic activity decreases as a result of lower oxygen availability (as noted previously) and the necessity to maintain cell membrane rigidity at higher temperatures. This may be a structural and functional response common to different phytoplankton phyla. The difference in temperature optima between these two models (16 °C vs. 25 °C) is likely due to the inclusion of ARA in Galloway & Winder's (2015) analysis. We found that ARA shows a positive relationship with temperature, and this likely increased the temperature optima of the LC-PUFA sum (ARA + EPA + DHA). However, taxonomy plays as much, if not more, of a role on FA production (Galloway & Winder, 2015), so the details of these changes will vary among taxa and will be further influenced by the expression and activity of desaturases (Guschina & Harwood, 2006).

The linear regression models also allowed us to make approximate predictions on potential reductions in n-3 LC-PUFA production based on specific increases in water temperature due to global warming. The mean temperature of all FA profiles in the data set ($n = 952$) was 19.8 °C; therefore, we started our base calculation at 20 °C. The IPCC climate change scenario A2 indicates a 1.3–4.5 °C increase in surface air temperature predicted up to year 2100 (Houghton *et al*., 2001). Our data set, which contains a global distribution of phytoplankton, predicts that a global average estimate of 2.5 °C increase in water temperature could result in reductions of 8% and 28% for EPA and DHA, respectively. The mean of these estimates (~18%) is close to other model projections that indicate a 12% reduction in n-3 LC-PUFA supply as a result of increasing sea surface temperature (Pethybridge *et al*., 2015). Diatoms, in particular, which contribute to most of the world's supply of EPA and DHA, may show a 6% reduction in

EPA and 7% reduction in DHA production with a 2.5 °C increase in water temperature. The quantity of EPA produced in the oceans by diatoms globally was recently estimated at 240 Mt annually (Budge *et al.*, 2014). We combined this estimate with our linear model to predict the change in global production of EPA due to an increase ocean temperature from 20 °C to 22.5 °C. Our model indicates that a 6% reduction in EPA production by diatoms equates to a 14.2 Mt loss of EPA annually. The current supply of EPA is barely sufficient to meet the nutritional demand of the current human population (Budge *et al.*, 2014). Further, diatoms cultured under elevated CO_2 conditions, which go hand in hand with increases in water temperature as a result of climate change, produced a ratio of LC-PUFA to SFA that was three times lower compared with present-day CO_2 levels (Rossol *et al.*, 2012). This reduction in diatom n-3 LC-PUFA production translated directly to copepods via trophic transfer, which constrained their growth and reproduction, demonstrating that ocean acidification can act in concert with temperature increases to negatively impact n-3 LC-PUFA production and transfer in aquatic food webs (Rossol *et al.*, 2012). Copepods were also found to lower their DHA content in response to elevated temperatures (outside their normal range), regardless of food resources available (Werbrouck *et al.*, 2016). This foretells negative effects for higher trophic levels as n-3 LC-PUFA are known to be progressively accumulated in aquatic food chains (Kainz *et al.*, 2004). Therefore, climate warming and ocean acidification, combined with an increasing human population, may impact continued access (and not only for humans) to these vital nutritional resources.

That the global n-3 LC-PUFA supply may be threatened in the future adds to a list of serious consequences as a result of climate warming. While experimental laboratory studies have shown that changes in FA composition can occur rapidly (<2 h) in response to temperature (Rousch *et al.*, 2003; Fuschino *et al.*, 2011), it is the predicted long-term, consistent decrease in n-3 LC-PUFA that may have the most lingering effects on food webs. In addition to rising temperatures, other environmental conditions related to climate change, such as eutrophication (i.e., excess nitrogen and phosphorus) and light intensity, may also affect global LC-PUFA availability, either directly or indirectly by affecting temperature (Piepho *et al.*, 2012). Terrestrial and aquatic wildlife depend heavily on aquatic resources for their n-3 LC-PUFA supply (Gladyshev *et al.*, 2009; Hixson *et al.*, 2015; Twining *et al.*, 2015). Humans are resourceful and technologically advanced; we will likely create new ways to meet our n-3 LC-PUFA needs (at least for those of us with the means). However, without this advantage, the remaining organisms on the planet, particularly those that normally have access to a significant supply of n-3 LC-PUFA, may have difficulty adapting to reduced levels. This could result in lower growth and/or reproduction rates, health issues like lowered immune system function resulting in a higher susceptibility to disease, and impaired cognitive abilities, particularly among top predators for which n-3 LC-PUFA are considered essential nutrients.

Our data synthesis suggests that increasing water temperature due to climate warming will lower EPA and DHA contents in major groups of phytoplankton, particularly diatoms and cryptophytes, which may have cascading effects in aquatic and terrestrial food webs. Further experimental and/or modeling research is needed to confirm these data synthesis findings to fully understand and predict the effect of global warming on LC-PUFA production in phytoplankton, as well as the subsequent movement of these vital compounds through aquatic and terrestrial ecosystems.

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Author contributions

SMH collected and analyzed the data. SMH and MTA interpreted the data and co-wrote the paper; MTA developed the initial concept and designed the research approach.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Linear regression models for phytoplankton groups, with temperature as a covariate to phytoplankton FA composition.
Table S2. Correlations between water temperature and fatty acid composition in various general of phytoplankton, presented as Pearson's correlation coefficient.
Table S3. Differences in phytoplankton fatty acid composition due to temperature, according to SIMPER. For each group, temperature was divided into four quartiles, where T1 is low, T2 is medium-low, T3 is medium-high and T4 is high temperature.
Table S4. Effect of phylogeny, geographic origin, and temperature on FA composition in phytoplankton (*P*-values).
Table S5 Fatty acid, temperature, and geographic origin data in species of Diatoms.
Table S6. Fatty acid, temperature, and geographic origin data in species of Chlorophytes.
Table S7. Fatty acid, temperature, and geographic origin data in species of Cryptophytes.
Table S8. Fatty acid, temperature, and geographic origin data in species of Haptophytes.
Table S9. Fatty acid, temperature, and geographic origin data in species of Dinophytes.
Table S10. Fatty acid, temperature, and geographic origin data in species of Cyanobacteria. .