A Fundamental Dichotomy in Long-Chain Polyunsaturated Fatty Acid Abundance between and within Marine and Terrestrial Ecosystems

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Abstract

Polyunsaturated fatty acids (PUFA), especially long-chain (i.e. ≥ 20 carbons) polyunsaturated fatty acids (LC-PUFA), are fundamental to the health and survival of marine and terrestrial organisms. Therefore, it is imperative that we gain a better understanding of their origin, abundance, and transfer between and within these ecosystems. We evaluated the natural variation in PUFA distribution and abundance that exists between and within these ecosystems by amassing and analyzing, using multivariate and analysis of variance methods, >3,000 fatty acid (FA) profiles from marine and terrestrial organisms. There was a clear dichotomy in LC-PUFA abundance between organisms in marine and terrestrial ecosystems, mainly driven by the C_{18} PUFA in terrestrial organisms and omega-3 (n-3) LC-PUFA in marine organisms. The PUFA content of an organism depended on both its biome (marine *vs* terrestrial) and taxonomic group. Within the marine biome, the PUFA content varied among taxonomic groups. PUFA content of marine organisms was dependent on both geographic zone (i.e. latitude; and thus broadly related to temperature) and trophic level (a function of diet). The contents of n-3 LC-PUFA were higher in polar and temperate marine organisms than those from the tropics. Therefore, we conclude that, on a per capita basis, high latitude marine organisms provide a disproportionately large global share of these essential nutrients to consumers, including terrestrial predators. Our analysis also hints at how climate change, and other anthropogenic stressors might act to negatively impact the global distribution and abundance of n-3 LC-PUFA within marine ecosystems and on the terrestrial consumers that depend on these subsidies.

Keywords: climate change, food webs, omega-3, polyunsaturated fatty acids, trophic ecology

Introduction

Fatty acids (FA) are the building blocks of structurally- and functionally-important lipid molecules (e.g. triacylglycerols, phospholipids) found in all organisms. Their production and distribution varies among plants and animals, and among biomes. A subset of FA, the long-chain (i.e. ≥ 20 carbons long) polyunsaturated fatty acids (LC-PUFA), are known to have key physiological functions in all vertebrate organisms, specifically involved in supporting neurological development and function, cardiovascular health, visual acuity, growth, reproduction, and the immune system (Brenna et al. 2009; Simopoulos 2011; Swanson et al. 2012; Calder 2015). The LC-PUFA are also critically involved in maintaining structure and fluidity in cell membranes (Arts and Kohler 2009). In particular, eicosapentaenoic acid (EPA; 20:5n-3), docosahexaenoic acid (DHA; 22:6n-3), and arachidonic acid (ARA; 20:4n-6) have distinct and vital functions in vertebrates. EPA has anti-inflammatory effects, lowers the risk of cardiovascular disease, positively influences immune functions and defense against infections, and may protect against some cancers (reviewed by Calder 2015). DHA is directly involved in several processes in the brain including, neurotransmission, cell survival, and prevents neuro-inflammation (and thereby mood and cognition, Bazinet and Laye 2014), and also acts as a precursor for docosatrienes, involved in anti-inflammation (Hong et al. 2003). ARA is also crucial for brain functioning, cell signalling, and is a precursor for endocannabinoids (Turcotte et al. 2015) and eicosanoids (Calder 2015). Thus, together, these three LC-PUFA form an important foundation for health and, by extension, survival in vertebrates.

There are large differences in the LC-PUFA composition of terrestrial and aquatic primary producers (Hixson et al. 2015; Twining et al. 2016). This inherent difference in LC-PUFA production at the base of aquatic and terrestrial food webs has important physiological

consequences for consumers. The LC-PUFA are mostly synthesized by primary producers at the base of aquatic food webs (e.g. diatoms, dinoflagellates, cryptophytes; Brett and Müller-Navarra 1997, Taipale et al. 2013; Galloway and Winder 2015). They are progressively consumed, and generally selectively retained, by other aquatic organisms higher up in the food chain (e.g. zooplankton, benthic invertebrates, molluscs, and fish; Dalsgaard et al. 2003; Iverson et al. 2004; Kainz et al. 2004; Budge et al. 2006; Hixson et al. 2015). The LC-PUFA are selectively retained at higher trophic levels; even small animals that have limited lipid storage capacity, under strong selection pressure retain these important compounds from their diet (Kainz et al. 2004; Schlechtriem et al. 2006; Twining et al. 2016). While vertebrates can synthesize their own LC-PUFA from their dietary precursors (ALA and LNA), the rate of synthesis is generally limited (Cook and McMaster 2004; Tocher et al. 2006); therefore, consuming EPA, DHA, and ARA pre-formed in the diet is highly advantageous for many vertebrates (Arts et al. 2001; Parrish 2009).

Freshwater ecosystems are known to be rich in n-3 PUFA, particularly EPA and DHA, in comparison with terrestrial ecosystems (Hixson et al. 2015; Twining et al. 2016). While the abundance and distribution of marine-derived LC-PUFA has been the focus of a plethora of studies for decades (e.g. Brockerhoff et al. 1963; Ackman et al. 1968; Dalsgaard et al. 2003; Budge et al. 2006; Arts et al. 2009; Parrish et al. 2013), a more global inventory of marine organism PUFA contents has yet to be compiled.

Aquatic organisms require cell membrane FA of varying chain lengths and numbers of double bonds to adapt to ambient water temperatures (Sinensky 1974; Cossins and Prosser 1978; Arts and Kohler 2009). This raises the question, is latitude (as a proxy for temperature) associated with distinct PUFA patterns in marine organisms and, if so, are there climate change implications? This distinction in PUFA content among marine latitudinal zones has been shown

in certain taxa, such as phytoplankton (Hixson and Arts 2016), macrophytes (van Ginneken et al. 2011), and zooplankton (Kattner and Hagen 2009); however, it has not been documented considering the marine biome as a whole.

While it has been established that there is a distinct functional dichotomy in the LC-PUFA production and abundance between freshwater and terrestrial ecosystems (Hixson et al. 2015), there is also a need to quantitatively establish this distinction between marine and terrestrial ecosystems. The n-3 and n-6 PUFA (ALA, EPA, DHA, and LNA and ARA, respectively) are of special interest due to their essentiality and physiological functions in organisms (Parrish 2009); therefore, we focused on these PUFA. The primary objective of this study is to quantify differences in PUFA among marine and terrestrial organisms, at varying trophic levels, to more rigorously document and quantify the distinct and natural variation in PUFA distribution and abundance that exists between and within these ecosystems.

Methodological approach

Data collection

Fatty acid data from marine and terrestrial organisms were collected from the primary, peer-reviewed, scientific literature. Articles were located and retrieved using the following citation indexing services: Google Scholar©, Web of Science©, and Scholars Portal©. The following search terms were used in combination with "fatty acids": marine, terrestrial, phytoplankton, macrophytes, zooplankton, bivalves, gastropods, annelids, echinoderms, crustaceans, cephalopods, fish, marine mammals, plants, insects, terrestrial mammals. In addition to the data derived from these searches we also used the marine phytoplankton FA profiles from Hixson and Arts (2016) and bird FA profiles from Galván et al. (2015).

To qualify for inclusion in the data set, the data were required to be species-specific, sampled from either muscle tissue (the greatest tissue mass in the body) or the whole body, and the animals were not cultured (with the exception of cultured phytoplankton and macrophytes). Each study must have presented all FA of interest: ALA, LNA, EPA, DHA, ARA; as well as the sums of saturated FA (SFA), monounsaturated FA (MUFA), and PUFA (or total FA along with a complete list of FA to calculate these sums). The FA data must also have been presented as proportional data, i.e. individual FA as a percentage of total FA from total lipids (or the calculated mean of neutral and polar lipid); referred to as "FA content" hereafter. Although it would have been preferable to perform a data synthesis on FA contents expressed as mass-fractions (mg FA g^{-1} wet or dry weight tissue extracted), the majority of studies (>75%) present FA data on a proportional basis (i.e. %). A Grubb's outlier test was used to determine if there were significant outliers ($p < 0.05$) for each FA within a particular group. If a significant outlier was detected (which occurred 8 times in the entire data set), the data entry was removed from the dataset.

Dataset

The FA data, for marine and terrestrial organisms, were sorted into 14 major taxonomic groups. The marine organisms comprised the following 11 taxonomic groups: phytoplankton, macrophytes, zooplankton, bivalves, gastropods, annelids, echinoderms, crustaceans, cephalopods, fish, birds, and marine mammals. The terrestrial taxa were sorted into 4 major taxonomic groups (plants, insects, birds, and terrestrial mammals). Complete FA data on other terrestrial vertebrates, such as reptiles and amphibians, are scarce in the literature, and thus were not included. In order to investigate patterns within either marine or terrestrial food webs, the above-mentioned groups were pooled, as follows, based on their approximate trophic position.

Primary producers consisted of phytoplankton, macrophytes, and terrestrial plants. Herbivores/omnivores consisted of annelids, bivalves, herbivorous/omnivorous crustaceans, zooplankton, and herbivorous/omnivorous terrestrial mammals. Carnivores consisted of cephalopods, carnivorous crustaceans, carnivorous fish, marine mammals, and carnivorous terrestrial mammals. The marine FA data were also sorted by geographic origin. This was determined by the location where the organism was sampled (as listed in the original primary article), and which was characterized by three latitudinally-defined geographic zones: polar (90-60ºN and S), temperate (60-30ºN and S), and tropical (30ºN to 30ºS). In cases where algal 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 the known global distribution (range) of that algal species. Algae were considered 'cosmopolitan' when they were listed as occupying two or more, of our three, latitudinal zones.

Analysis of Variance

ANOVA models were used to determine whether biome, taxonomic group, latitudinal zone, and/or trophic level could account for the variance in FA content among the organisms in our dataset. Biome (a fixed categorical variable) included 2 groups (marine or terrestrial). Taxonomic group (also a fixed categorical variable) included 11 groups in the marine biome (see above) and 3 groups in the terrestrial biome (see above). Latitudinal zone (a random categorical variable) was characterized by three geographic regions (see above). Trophic level (a random categorical variable) had three levels: primary producers, herbivore/omnivores, and carnivores, as above. A nested ANOVA was used to determine the effect of latitudinal zone within taxonomic group.

Using a combination of the above factors, 6 statistical models (using Minitab Statistical Software version, 17) were tested on each individual PUFA or FA group (e.g. SFA, MUFA, PUFA) to determine the effects and/or interactions among biome, taxonomic group, latitudinal zone, and trophic position on FA content (Table 5). The categorical factors were considered to have significant effects on FA proportions and/or distributions when $p < 0.05$, and, where significant differences occurred, treatment means were further differentiated using the Tukey HSD multiple comparison test, with Bonferroni corrections. The residuals from each model were examined to ensure there were no violations of model assumptions. Plots of residuals were evaluated for model assumptions: homogeneity of variance (plot of residuals *vs* fitted values), normality (frequency of residuals, normal probability plot), and independence assumptions (residuals *vs* lag +1 residuals). Levene's test was also used to evaluate equal variances.

Multivariate analyses

All multivariate analyses were conducted using PRIMER-E (Plymouth Routines in Multivariate Ecological Research; PRIMER-E Ltd, version 7.0.10, Ivybridge, UK). Principal coordinates analysis (PCO) was used to visualize and quantify patterns observed among FA profiles (individual PUFA and the sums of SFA, MUFA, and PUFA) of organisms depending on their biome (marine or terrestrial), taxonomic group (see above), and approximate trophic level (see above). To evaluate the significance of the apparent biome, taxonomic group, and trophic level separation observed in the PCO, we used a one-way permutational multivariate analysis of variance (PERMANOVA) on the same FA dataset. The PCO was used on the entire data set of PUFA and FA groups (in both marine and terrestrial organisms), as well as the marine data subset, the terrestrial data subset, and the phytoplankton and fish data subsets. The FA vectors included all those in the analysis, listed above.

The similarity in percentages (SIMPER) routine was used to differentiate FA profiles based on biome and taxonomic group. The similarity coefficient in SIMPER ranges from 0 to 100% with the ends of the range representing the extreme possibilities, i.e. S = 0% if two samples are totally dissimilar and S = 100% if two samples are totally similar. The non-metric Bray-Curtis dissimilarity statistic was used to quantify the compositional dissimilarity between samples in the PCO and SIMPER (Bray and Curtis 1957). This test delivers robust and reliable dissimilarity results, and is one of the most commonly used metrics to explore relationships in ecology, environmental sciences and related fields (Clarke and Warwick 2001). A permutation of homogeneity of dispersions (PERMDISP) was used to test the homogeneity of multivariate dispersions within groups. Significant differences in dispersion within taxonomic groups were observed ($p = 0.001$); therefore, data were square root transformed prior to multivariate analysis (Greenacre and Primicerio 2013; Hixson et al. 2015).

Data synthesis results

Database

A total of 3,072 FA profiles were collected from marine and terrestrial organisms which were subsequently divided into biomes (Table 1), taxonomic groups (Table 2), and latitudinal zones (in the case of marine organisms only; Table 3). The data set used in the analyses is provided in the Supplementary Data.

ANOVA results

Both biome and taxonomic group, and the interaction between them, significantly determined the FA content of organisms (Table S1). The single exception was that taxonomic group did not determine SFA; however, because the interaction between biome and taxonomic

group was significant for SFA, taxonomic group could not be interpreted alone (Table S1). Trophic level determined PUFA and FA groups, as values tended to increase or decrease with increasing trophic level in both biomes (Table 4). This pattern was most striking in ALA, LNA, and DHA when compared between marine and terrestrial organisms (Fig. 1). ALA plus LNA decreased with increasing trophic level, but the magnitude of the change was different in marine and terrestrial ecosystems. DHA was not observed in terrestrial plants, and was also not recorded in insects (Table 1, Fig. 1). DHA content generally increased from primary producers to carnivores in marine ecosystems, with carnivores having significantly higher proportions than the other groups (Fig. 2a). ARA was higher in terrestrial organisms compared to marine organisms (Table 4). Within the marine ecosystem, herbivores/omnivores had higher EPA (Fig. 2b) and ARA contents (Fig. 2c) than primary producers and carnivores. ARA contents varied greatly among taxonomic groups within either ecosystem, and were notably high in macrophytes, gastropods, echinoderms, and insects (Table 1).

Latitudinal zone explained the variation in PUFA content for all PUFA and FA summary categories in marine organisms, except ALA and LNA (Table S2). Taxonomic group within marine environments also determined FA content (two-way ANOVA). Within each taxonomic group, latitudinal zone remained a significant factor in FA content of marine organisms, regardless of grouping (nested ANOVA; Table S3). In addition to latitudinal zone (except for ALA and LNA), individual PUFA content also depended on trophic level, and generally increased with higher trophic levels (Table S4, S5; Fig. 3). A nested ANOVA revealed that taxonomic group within each trophic level determines FA content ($p < 0.05$ for all FA, except ALA; Table S6), not just trophic level alone ($p > 0.05$ for all FA).

206 **Multivariate analyses results**

207 There was a clear separation, using PCO, between marine *vs* terrestrial individuals along
208 PCO1 (Fig. 4), confirming that biome was a significant factor in the similarity matrix, according
209 to the PERMANOVA design (F= 1110.6; p = 0.001; number of permutations= 999). The
210 ordination explains 62.4% of the variation; PCO1 explained most of the total variation (40.3%),
211 and PCO2 explained another 22.1%. The FA vectors along PCO1 indicated an association
212 among EPA, DHA, and ARA with marine organisms, and ALA and LNA with terrestrial
213 organisms. Along PCO2, SFA and MUFA showed an opposing relationship to PUFA (this was
214 expected as these sums add up to 100%), but did not divide the plot according to the biome
215 factor imposed in this particular plot.

216 PCO explained 51.8% of the total variation (PCO1 = 30%, PCO2 = 21.8%) in the FA
217 content of marine organisms as a function of latitudinal zone. Taxonomic group ($F = 6.31$; $p < 0.001$), latitudinal zone ($F = 18.8$; $p < 0.001$), and the interaction between taxonomic group and
218 0.001), latitudinal zone ($F = 18.8$; $p < 0.001$), and the interaction between taxonomic group and
219 latitudinal zone ($F = 5.03$; $p < 0.001$) were significant factors in the Bray-Curtis similarity matrix
220 according to PERMANOVA (with 999 unique permutations). Using marine phytoplankton as a
221 subset, the ordination explained 80.8% of the total variation, with PCO1 explaining most of the
222 variation (52.4%), and PCO2 the remainder (28.4%). The PERMANOVA analysis revealed that
223 latitudinal zone ($p = 0.002$), taxonomic group ($p= 0.001$), and the interaction between zone and
224 group ($p= 0.001$) were significant factors in the Bray-Curtis similarity matrix. For marine fish
225 (Fig. 5), the ordination explained 74.3% of the total variation (PCO1 explained 55.7%, and
226 PCO2 explained 18.6% of the variation). Latitudinal zone was a significant factor in the Bray-
227 Curtis similarity matrix according to PERMANOVA ($F= 16.0$; $p= 0.001$; with 999 unique
228 permutations). Within the terrestrial organism data set, PCO1 explained 40.5% of total variation,

and PCO2 explained 19.5% (Fig. 6). Taxonomic group was a significant factor in the Bray-Curtis similarity matrix according to PERMANOVA ($F= 113.2$; $p= 0.001$; with 995 unique permutations). The FA vectors along PCO1, DHA and ARA, indicated an association with birds and mammals, as opposed to plants and insects. Conversely, ALA, LNA, and PUFA were associated with plants and insects along PCO1.

SIMPER analysis revealed that within the marine data set, macrophytes and marine mammals were the most dissimilar pair based on their FA content (30.8% dissimilar), while fish and zooplankton were the most similar pair (16.1%). In both comparisons, MUFA caused the most variation between groups. Within taxonomic groups, phytoplankton were the most diverse in terms of FA content (71.8% similarity within the group) and marine mammals were the most similar (88.2% similarity within the group). Dispersion among groups was not homogenous ($p = 0.001$) according to PERMDISP, which is partially explained by unequal sample sizes among taxonomic groups, with some groups (such as phytoplankton) with a large number of samples ($n = 505$) and large dispersion and higher variation. Within the marine data set, latitudinal zones were equally dissimilar (22.6-23.7%). DHA caused the greatest dissimilarity between temperate and tropical marine organisms, while MUFA caused the most dissimilarity between polar and tropical or temperate marine organisms. Within the terrestrial data set, plants and mammals were the most dissimilar (34.5%), followed by plants and birds (33.2%), insects and mammals (30.6%), plants and insects (29.3%), insects and birds (29.1%) and birds and mammals (25.8%). LNA and ARA caused the most dissimilarities among all terrestrial groups compared.

Summary and Perspective

Data synthesis

Our data synthesis, consisting of 3,072 FA profiles from marine and terrestrial organisms, allowed us to uncover a striking dichotomy in the distribution and abundance of PUFA between marine and terrestrial ecosystems. This contrast was primarily driven by the n-3 LC-PUFA (EPA, DHA) content in marine organisms, compared with terrestrial organisms (which contained higher levels of the C_{18} PUFA ALA and LNA; Fig. 4). Marine organisms also had higher total n-3 PUFA contents, while terrestrial organisms had typically high total n-6 PUFA contents. While the FA content of marine organisms has been documented for hundreds of individual species, and the comparison between freshwater and terrestrial organisms has been established (Hixson et al. 2015), this is the first time FA composition in marine and terrestrial ecosystems has been compared in a comprehensive quantitative study.

Our data set represented 14 taxonomic groups distributed among marine and terrestrial ecosystems. While our data collection was as thorough as possible, FA profiles for marine organisms were much more prevalent in the literature than those for terrestrial organisms, and within marine organisms, certain taxa were better represented than others (often based on their relevance to human consumption; e.g. bivalves and fish). Grouping species together (i.e. by taxonomic group and/or trophic level) also introduced a degree of variability, as phylogeny is a known driver of FA content (Budge et al. 2002; Dalsgaard et al. 2003; Makhutova et al. 2011; Galloway and Winder 2015; Hixson et al. 2015). While we organized taxonomically and by trophic level in order to aid in the detection and interpretation of FA patterns among them, there is still marked variation in a single species within a taxonomic group because of an organism's specific habitat, feeding preferences, gender, life stage, etc., even when these species shared the

same biome and had similar diets (according to trophic position). This introduced variation into our analysis. However, despite species differences, the variation within groups was minimal compared to the differences between groups, particularly between biomes. Our main conclusion is that a fundamental dichotomy exists in the relative abundance, and therefore global distribution, of PUFA between marine and terrestrial organisms.

Dichotomy between ecosystems

The difference in FA content between marine and terrestrial organisms is evident when observed visually in multivariate space (Fig. 4). This disparity is mainly driven by the LC-PUFA (EPA, DHA, and ARA) in marine organisms, and the C_{18} PUFA (ALA and LNA) in terrestrial organisms. This difference in FA content between the two ecosystems has its primary origin at the base of the food webs. In terrestrial ecosystems, ALA was the only n-3 PUFA recorded in primary producers (vascular plants) in our data set (although they are also known to produce other n-3 PUFA, such as 16:3n-3 and 18:4n-3: Dubois et al. 1997). By contrast, in marine ecosystems, primary producers (phytoplankton and macrophytes) predominantly contained n-3 LC-PUFA (EPA and DHA). In addition, our analyses revealed that marine primary producers synthesize, on average, ~1.7× more n-3 PUFA (of the reduced subset of PUFA we analyzed here) than terrestrial primary producers. Our data analysis highlights that marine primary producers consist of 13-17% dietary n-3 LC-PUFA on average, which is available to subsequent consumers (Table 1), whereas such an n-3 LC-PUFA supply is entirely missing (at least in the plants we surveyed) from terrestrial primary producers. Further, we found that in marine organisms the n-3 PUFA dominate over n-6 PUFA; while the opposite is true for terrestrial organisms, which has also been observed when comparing terrestrial with freshwater organisms (Skjervold 1992; Koussoroplis et al. 2008; Hixson et al. 2015). Within each biome, taxonomic

group played an important role, and so did the interaction between an organism's biome and their taxonomic group. Thus, the FA content of a particular organism depends on both an organism's location (land *vs* ocean), and the taxonomic group to which it belongs.

The overall FA composition in organisms has been confirmed experimentally to also depend on their diet (Iverson et al. 1997; Lane et al. 2006; Koussoroplis et al. 2008; Torres-Ruiz et al. 2010) and has been reviewed (Iverson et al. 2004; Budge et al. 2006; Kelly and Scheibling 2012). We found that within each biome, individual PUFA tend to either increase or decrease as a function of an organism's trophic level, as well as habitat. For example, the sum of ALA and LNA generally decrease with increasing trophic level (Fig. 1), but are higher in terrestrial food webs than marine. On the other hand, DHA tended to increase with increasing trophic level, at least in the marine ecosystem (Figs. 1, 2, 3). This result was also observed between terrestrial and freshwater organisms (Hixson et al. 2015). Interestingly, while SFA content depended on approximate trophic level, it was not different between biomes.

Similarly, to what was observed in our marine data set, other researchers have also observed that DHA was transferred and selectively retained in the aquatic food web, and generally increased in higher trophic levels (Kainz et al. 2004; Persson and Vrede 2006; Koussoroplis et al. 2008; Hixson et al. 2015; Twining et al. 2016). The essential PUFA are transferred along trophic levels at about twice the efficiency of bulk carbon (Gladyshev et al. 2011; Hartwich et al. 2013), and they are thereby generally retained, rather than diluted, in the biomass of organisms of higher trophic levels; a characteristic known in freshwater ecosystems (Gladyshev et al. 2013; Hixson et al. 2015; Twining et al. 2016). This is because DHA (and, to a lesser extent EPA) is minimally modified from ingestion to assimilation, and generally conserved in its original form to serve specific and important physiological purposes, rather than

being catabolized and/or modified (Kainz et al. 2004; Twining et al. 2016). However, it is worth noting that this pattern may be further modified by taxonomic affiliation, as organisms may share a similar trophic position (e.g. cladocerans and copepods), but have markedly different DHA contents. Ultimately, it is taxonomic group within each trophic level that is the most important determinant, as shown in the nested ANOVA model. Conversely, C_{18} PUFA (ALA and LNA) generally decrease with increasing trophic level (in both aquatic and terrestrial ecosystems), which suggests that ALA and LNA are utilized either as precursors for the LC-PUFA or catabolized, rather than being retained in tissues.

In terrestrial ecosystems, the EPA and DHA content in carnivores originated either directly from aquatic food sources (see above) or is produced endogenously; although the rate of synthesis from ALA is typically very low in vertebrates (Brenna et al. 2009; Domenichiello et al. 2015). Within the terrestrial ecosystem, the FA contents of mammals and birds were different from terrestrial plants, on account of the difference in LNA (higher levels found in plants) and DHA (not found in the plants in our data set; Fig. 6). The ability for vertebrates to either access aquatic food sources, or modify ALA becomes important for survival. Therefore, we conclude that terrestrial ecosystems are, in general, a much less important source of n-3 LC-PUFA production than aquatic ecosystems, and that aquatic organisms (both marine and freshwater), through a variety of pathways (Gladyshev et al. 2009), provide an important nutrient subsidy to terrestrial organisms. The availability of rich sources of EPA and DHA is critical for many terrestrial vertebrates, and the timing and quantity may be important as well. For example, shorebirds are known to gorge on n-3 LC-PUFA marine resources for long distance migration, i.e. n-3 LC-PUFA are used as ‘performance enhancing substances’ to prepare muscles for migration (Maillet and Weber 2006; Guglielmo 2010).

Fatty acid dynamics in food webs

The LC-PUFA have different physiological functions, may be metabolized and incorporated into tissues differently, and may vary in terms of importance in nutritional requirements for different species (Emery et al. 2016). We found that individual PUFA contents varied as a function of the biome of the organism and/or their approximate trophic position in the food chain. Generally, we found that FA tended to increase or decrease with increasing trophic level (Fig. 2), although this was not always the case. For example, relative EPA content increased from marine primary producers to herbivores/omnivores, but decreased from herbivores/omnivores to carnivores. Some of the herbivores/omnivores in our marine data set were zooplankton, which have been shown to exhibit an EPA-retentive metabolism (Kainz et al. 2004; Wacker and Martin-Creuzburg 2007; Hartwich et al. 2013). EPA is highly retained in zooplankton, whereas DHA is highly retained in most fish (e.g. salmonids; Kainz et al. 2004), which explains the different relationships we observed between EPA and DHA in our data. In fish, for example, there is increasing evidence to support the observation that EPA is preferentially catabolized or further converted to DHA (e.g. in salmonids; Murray et al. 2014) rather than spared and retained in tissues, and as such, EPA appears to be generally more dispensable compared to DHA (Trushenski et al. 2012; Glencross et al. 2015; Emery et al. 2016). This was observed in our dataset which documented a decrease in EPA content in carnivores. It has been suggested that DHA (and ARA), are the primary drivers of LC-PUFA essentiality in some fish species (Trushenski et al. 2012; Rombenso et al. 2016). This may be the case in other aquatic vertebrates and semi-aquatic mammals as well (Koussoroplis et al. 2008), as we observe selective retention in DHA up to carnivores, coupled with a significant drop in EPA content. Therefore, it appears that EPA and DHA are required in different proportions by different

consumers, and together are not necessarily progressively retained from primary producers up to carnivores, although this is highly dependent on species.

Fatty acid abundance and distribution within marine ecosystems

The diversity of organisms in our data set allowed us to take a quantitative approach in defining similarities and differences in the abundance and distribution of FA within the marine ecosystem. Marine macrophytes and marine mammals had the most dissimilar FA profiles, while fish and zooplankton had the most similar FA profiles. In both comparisons, MUFA was the underlying source of most of the variation between groups. This distinction is important, as individual MUFA are often recognized as biochemical markers in marine food webs, and are frequently used to quantitatively document predator-prey interactions (Iverson et al. 2009). Beyond diet, taxonomy is an important factor that defines FA content in marine organisms (Gladyshev et al. 2013; Galloway and Winder 2015). Species grouped in similar, yet broad taxonomic classifications did not necessarily possess the same FA content as one another. For example, we found that phytoplankton were the most diverse group in terms of FA content. Dispersion among taxonomic groups was not homogenous, which can be partially explained by unequal sample sizes, with some taxa (such as phytoplankton), that had a large number of samples, showing a large dispersion and higher variation. Ultimately, we found that assuming the trophic level of an organism (as a function of diet, as shown by Iverson et al. 2004; Budge et al. 2006) could be used as a tool to roughly estimate FA content. However, it is taxonomic group within each trophic level that is a more important determinant (Galloway and Winder 2015), as shown in the nested ANOVA model.

Fatty acid differences in marine ecosystems defined by latitude

Temperature directly influences metabolism, functioning, and survival in aquatic organisms (Gaston 2003). In an attempt to maintain physiological homeostasis when faced with temperature changes (Clarke 2003), ectotherms may change the structure of their cell membrane by modifying FA chain length and degree of unsaturation in membrane lipids to maintain a desired level of order (fluidity) in cell membranes (Sinensky 1974; Guschina and Harwood 2006; Arts and Kohler 2009). In order to maintain fluidity in cold waters, ectotherms tend to retain or increase the content of membrane PUFA, as the double bonds enhance the ability of FA to "bend" and increase membrane fluidity (Hazel 1995; Arts and Kohler 2009; Sperfeld and Wacker 2012; Parrish 2013). Therefore, using latitude (as a proxy for habitat temperature) to quantitatively define the FA content of marine organisms was of interest. We found that geographic zone, taxon, and trophic level synergistically determined the FA content of marine organisms. The C_{18} PUFA (ALA and LNA) content in marine organisms did not differ by geographic zone. These PUFA are essential to animals regardless of latitude; however, they differed quantitatively among taxa and trophic level.

Generally, it is assumed that LC-PUFA, especially EPA and DHA, are less prevalent or abundant in tropical marine ecosystems compared to polar marine ecosystems, where EPA and DHA are known to be in rich and abundant supply (Lands 1982; Broadhurst et al. 2002). Tropical organisms tend to possess FA profiles that are somewhat different from those of temperate and polar regions (Ahlgren et al. 2009; Iverson et al. 2009). For example, in polar oceans, marine organisms characteristically contain relatively high levels of MUFA (particularly 20:1 and 22:1), which are often regarded as biomarkers of zooplankton, such as krill and copepods (Brett et al. 2009) These MUFA are routinely transferred to higher trophic level

organisms. This was observed in the polar marine organisms in our data set (Table 3), including fish (Fig. 3), relative to tropical and temperate organisms.

We found that the relative proportion of n-3 LC-PUFA, total MUFA, and total PUFA were higher in organisms located in polar regions than those in tropical regions. This aligns with the hypothesis that cold-water ectotherms organize long-chain, unsaturated FA to maintain membrane fluidity in order to inhabit cold waters (Sinensky 1974; Arts and Kohler 2009). For this reason, having elevated n-3 LC-PUFA levels may be a mechanism used to survive in polar regions, where organisms typically live at temperatures near the freezing point for much of the year (Thomas and Dieckmann 2002). Both in macrophytes (van Ginneken et al. 2011) and microalgae (Boelen et al. 2013; Hixson and Arts 2016), PUFA content and degree of unsaturation in polar oceans were higher than in tropical oceans. Conversely, total SFA and ARA increase in marine organisms going from polar to tropical regions (assuming increasing temperature); a result also observed in a large data synthesis of phytoplankton (Hixson and Arts 2016) and macrophytes (van Ginneken et al. 2011). It is important to note that we did not consider depth as a factor within each latitudinal zone for all marine data, thus tropical organisms inhabiting deep waters may be subject to low temperatures, potentially increasing their n-3 LC-PUFA content. While we did not specifically account for this in our analysis, we estimated that our dataset of marine fish contained relatively equal proportions of deep-sea fish among the three latitudinal zones (polar 25.6%, temperate 29.2%, tropical 32.5%). Thus, our dataset did not have an undue bias towards “colder-water” deep-sea fish in tropical zones. Further, despite the slightly higher contribution of deep-sea fish in the tropical zone (potentially increasing the n-3 LC-PUFA content in tropical fish), the difference in LC-PUFA content among latitudinal zones is still

435 clearly evident. Thus our analyses yielded a conservative estimate of the observed differences
436 among fishes from different latitudinal zones, and especially between polar and tropical fish.

437 We found that both geographic zone (latitude) and diet (a function of trophic level) can
438 predict FA content in marine organisms. For DHA, carnivores contained the highest levels,
439 which demonstrates selective retention relative to primary producers (Fig. 3). While our results
440 demonstrate and support previous studies that found DHA is selectively retained along the food
441 chain (Kainz et al. 2004; Koussoroplis et al. 2008; Hartwich et al. 2013; Hixson et al. 2015), we
442 also found that FA content was highly dependent on the taxonomic affiliation of organisms, a
443 result which has been previously observed in the taxonomy of phytoplankton (Mourente et al.
444 1990; Galloway and Winder 2015; Hixson and Arts 2016), zooplankton (Persson and Vrede
445 2006), and benthic invertebrates (Parrish et al. 1996; Makhutova et al. 2011). It is not well
446 understood if the PUFA content of marine organisms, such as fish, is controlled by phylogenetic,
447 ecological, or trophic factors (Gladyshev et al. 2013); however, according to our analysis of
448 marine organisms in general, these factors are related and interactive.

449 **Fish in polar, temperate, and tropical waters**

450 Fish were of particular interest due to their importance as a protein source and ultimately
451 the main source of pre-formed LC-PUFA for terrestrial vertebrates (including humans). Fish
452 represent a major vector (subsidy) in the transfer of LC-PUFA from marine to terrestrial
453 ecosystems (Gladyshev et al. 2009, 2013). Furthermore, fish and shellfish production in marine
454 ecosystems will likely remain a key source of EPA and DHA for humans. Therefore, it is
455 important to identify and conserve geographic areas that have exceptionally high n-3 LC-PUFA
456 production and subsequent retention in fish. We found that latitudinal geographic zone
457 significantly determined FA content in fish in multivariate space (Fig. 5).

458 We observed separation of fish in polar and tropical marine zones, with fish in temperate
459 zones in between and dispersed within fish in tropical and polar zones, which created a
460 latitudinal gradient (Fig. 5). Generally, tropical ecosystems contain organisms with FA profiles
461 that are different from those in temperate and polar ecosystems (Iverson et al. 2009), and warm-
462 water fish contain less EPA and DHA, and more ARA compared to cold-water fish (Lands 1982;
463 Broadhurst et al. 2002; Kolakowska et al. 2006). The high MUFA levels we observed in polar
464 fish are likely a biomarker of zooplankton (copepods), as this taxonomic group is an important
465 link between lower and higher trophic levels (Parrish 2013). Typical of tropical ecosystems, prey
466 throughout these systems generally contain relatively high levels of n-6 LC-PUFA, and very low
467 levels of MUFA (Iverson et al. 2009).

468 We found that fish in polar and temperate marine zones provide the highest nutritional
469 value for human consumption in terms of n-3 LC-PUFA content. Ironically, some of the most
470 striking impacts of global climate change have been observed in polar oceans (Hoegh-Guldberg
471 and Bruno 2010), and it is known that these regions are particularly sensitive to changes in
472 temperature (Smetacek and Nichol 2005). At the base of marine food webs, the distribution,
473 abundance, and productivity of primary producers (i.e. phytoplankton) are changing in response
474 to eutrophication, warming, acidifying, and stratifying oceans, and the effects of these systemic
475 changes can cascade through food webs (Polovina et al. 2008; Doney et al. 2009). An increase in
476 water temperature due to climate change is predicted to result in decreased proportions of EPA
477 and DHA in a variety of organisms including phytoplankton (Hixson and Arts 2016), copepods
478 (Werbrouck et al. 2016), and albacore tuna (Parrish et al. 2015), as a result of cellular adaptation
479 (homeoviscous adaption) to warming waters. This indicates that the impact of warming waters

may alter FA content in consumers, not only through nutrient transfer, but also through their own biochemical response to temperature (Werbrouck et al. 2016).

Compounding these effects, climate change can also shift the normal geographic distribution of fish, and other species' populations, as they adapt to current ambient conditions (Stachowicz et al. 2002, Gamito et al. 2015). A rising number of non-polar species are already expanding their ranges into more polar areas (Hoegh-Guldberg and Bruno 2010). Tropical species are predicted to expand toward temperate regions, and temperate species in turn will move into polar regions (Cheung et al. 2009; Vinagre et al. 2011). The dominance of lipid-rich species (with high n-3 LC-PUFA contents) at high latitudes will probably decrease in response to this shift (Gamito et al. 2015). These shifts in population distribution and changes in FA quantity and quality in response to warming temperatures can ultimately affect the health-benefits of commercially-relevant species that inhabit the most sensitive regions to climate change.

Implications for consumers

Vertebrates (and most aquatic invertebrates) require DHA (and EPA to some extent) for optimal functioning (Arts et al. 2009; Calder 2015). Endogenous biosynthesis from ALA (or from other precursors, such as EPA or 22:5n-3) is generally limited in most vertebrates, including humans (Brenna et al. 2009). As our data synthesis shows that primary producers in marine and terrestrial ecosystems exert a high level of control over the distribution of EPA and DHA among higher trophic level organisms in their respective food webs. Ultimately EPA and DHA synthesized by aquatic primary producers make their way, by various vectors, to terrestrial organisms (including humans). These n-3 LC-PUFA are not produced in quantity by most plants in terrestrial food webs therefore, preformed EPA and DHA are generally not available to consumers from this source. While terrestrial predators usually cannot obtain EPA and DHA

503 from terrestrial plants, ultimately they can be derived from terrestrial ALA and subsequently
504 bioconverted, either by the predators themselves, or by their prey. This indirect route has
505 energetic costs, in terms of trophic efficiency, as well as the amount of ALA (from plants) and n-
506 3 LC-PUFA derived from their prey, because n-3 PUFA are not as prevalent in terrestrial
507 organisms compared to their aquatic counterparts. Thus the supply of preformed EPA and DHA
508 from aquatic organisms generally provides a more abundant and more efficient source of n-3 LC-
509 PUFA to terrestrial animals that have access to aquatic ecosystems (Gladyshev et al. 2009,
510 2013). Consumers that do not have access to aquatic resources, particularly primary consumers,
511 have undoubtedly faced strong selection pressure to modify ALA and LNA into LC-PUFA, as
512 the ability to synthesize the LC-PUFA is likely related to the inverse of access to these LC-
513 PUFA (Hixson et al. 2015).

514 **Conclusions**

515 We have illustrated a fundamental dichotomy in PUFA abundance and distribution
516 between marine and terrestrial ecosystems. Biome, taxonomy, and trophic level defined FA
517 content of organisms between (and within) ecosystems. Individual n-3 and n-6 PUFA showed
518 different relationships among trophic levels, indicating that EPA, DHA, and ARA are
519 functionally different, and are likely retained or catabolized differently as a function of taxonomy
520 and diet. In marine ecosystems, the n-3 LC-PUFA were higher in polar and temperate organisms
521 than those in the tropics. In particular, fish located in polar and temperate latitudes feature higher
522 levels of n-3 LC-PUFA than those in the tropics. Therefore, we conclude that cool water fish in
523 particular provide an important resource (i.e. essential n-3 LC-PUFA) to many consumers,
524 including terrestrial predators. Climate warming and other anthropogenic influences threaten LC-
525 PUFA production in marine ecosystems in a variety of ways. These factors include increasing

526 water temperatures and its effect on homeoviscous adaptation of cell membranes, biological
527 impacts such as eutrophication (which leads to algal communities being dominated by LC-
528 PUFA-impoverished cyanobacteria), novel species assemblages (i.e. redistribution of species),
529 overfishing (Hoegh-Guldberg and Bruno 2010), and increased absorption of anthropogenic CO_2
530 leading to ocean acidification (Bermúdez et al. 2015). Ultimately these human-induced changes
531 can impact the production, distribution, and transfer of EPA and DHA within the marine
532 ecosystem, and may eventually reduce their transfer (subsidy) to terrestrial ecosystems.
533 Therefore, in light of these effects it is becoming increasingly imperative to conserve our marine
534 resources so as to sustain adequate levels of n-3 LC-PUFA for our health, and for the health of
535 all animals on this planet.

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Figures and Tables

Table 1. Fatty acid content (% total fatty acids) of marine and terrestrial organisms (mean ± standard error).

Taxonomic group	LNA	ALA	ARA	EPA	DHA	∑SFA	∑MUFA	∑PUFA	∑n-3 FA	∑n-6 FA	DHA/EPA
Marine (n=2,063)											
Phytoplankton (n=504)	2.5 ± 0.2	3.5 ± 1.0	0.8 ± 0.1	11.9 ± 0.4	5.2 ± 0.3	37.0 ± 0.7	25.3 ± 0.5	35.4 ± 0.7	20.8 ± 1.1	3.3 ± 0.2	3.6 ± 0.5
Macrophytes (n=191)	6.2 ± 0.4	6.6 ± 0.5	8.6 ± 0.5	13.2 ± 1.0	0.2 ± 0.1	35.0 ± 1.0	19.8 ± 0.7	44.7 ± 1.1	20.1 ± 0.1	14.8 ± 0.6	0.05 ± 0.01
Zooplankton (n=139)	1.7 ± 0.1	1.6 ± 0.1	1.2 ± 0.2	16.2 ± 0.5	15.2 ± 0.7	24.9 ± 0.8	32.1 ± 1.5	44.6 ± 1.2	33.0 ± 1.1	2.9 ± 0.2	1.0 ± 0.05
Bivalves (n=242)	2.1 ± 0.1	1.8 ± 0.1	2.4 ± 0.1	14.6 ± 0.5	11.9 ± 0.5	30.7 ± 0.9	20.5 ± 0.6	46.2 ± 0.9	28.3 ± 0.8	4.4 ± 0.2	1.1 ± 0.1
Gastropods (n=118)	2.6 ± 0.2	2.4 ± 0.2	7.8 ± 0.5	10.0 ± 0.8	2.5 ± 0.5	30.9 ± 0.8	23.5 ± 0.6	41.6 ± 1.0	14.9 ± 1.0	10.4 ± 0.5	0.8 ± 0.2
Annelids (n=48)	5.2 ± 1.0	1.9 ± 0.3	2.2 ± 0.2	9.7 ± 1.0	3.3 ± 0.6	24.8 ± 0.9	32.8 ± 1.6	37.6 ± 1.8	14.9 ± 1.3	7.4 ± 1.0	0.3 ± 0.1
Echinoderms (n=106)	2.6 ± 1.2	1.4 ± 0.2	11.2 ± 0.7	13.0 ± 0.8	3.8 ± 0.4	26.2 ± 1.1	29.2 ± 0.9	41.4 ± 1.5	18.2 ± 1.0	13.8 ± 1.4	0.8 ± 0.4
Crustaceans (n=153)	1.9 ± 0.2	0.6 ± 0.1	4.6 ± 0.3	15.3 ± 0.6	10.7 ± 0.5	24.2 ± 0.8	28.7 ± 0.9	39.2 ± 1.1	26.7 ± 0.9	6.5 ± 0.4	0.8 ± 0.04
Cephalopods (n=118)	0.6 ± 0.1	0.3 ± 0.0	3.3 ± 0.3	12.8 ± 0.4	23.9 ± 0.9	28.2 ± 0.9	16.3 ± 1.1	44.7 ± 1.4	37.0 ± 1.2	4.0 ± 0.3	1.9 ± 0.1
Fish (n=239)	1.5 ± 0.1	0.9 ± 0.1	2.2 ± 0.2	7.7 ± 0.3	17.7 ± 0.6	29.2 ± 0.5	34.0 ± 0.8	34.9 ± 0.8	26.3 ± 0.7	3.7 ± 0.2	2.9 ± 0.1
Mammals (n=205)	1.6 ± 0.1	0.7 ± 0.1	1.0 ± 0.3	5.4 ± 0.2	7.9 ± 0.3	18.1 ± 0.4	55.6 ± 0.7	27.5 ± 1.1	14.1 ± 0.4	2.6 ± 0.3	1.7 ± 0.1
Terrestrial (n= 1,009)											
Plants (n=410)	38.4 ± 1.0	11.8 ± 0.8	0.5 ± 0.1	-	-	20.9 ± 0.8	26.6 ± 0.9	50.5 ± 1.0	11.8 ± 0.8	38.9 ± 1.0	-
Insects (n=389)	15.4 ± 0.7	13.4 ± 0.8	16.5 ± 2.9	1.3 ± 0.5	-	35.4 ± 1.0	35.8 ± 0.9	28.8 ± 1.0	14.7 ± 0.1	31.9 ± 2.6	-
Birds (n= 107)	9.96 ± 0.5	0.99 ± 0.1	8.18 ± 0.3	0.14 ± 0.0	3.75 ± 0.2	48.4 ± 0.5	25.6 ± 0.7	26.0 ± 0.6	6.3 ± 0.2	19.8 ± 0.6	37.5 ± 2.1
Mammals (n=193)	12.5 ± 0.8	5.6 ± 1.2	2.6 ± 0.5	0.9 ± 0.1	1.8 ± 0.3	40.3 ± 1.1	36.8 ± 1.1	22.5 ± 1.2	8.3 ± 0.6	15.1 ± 0.7	2.1 ± 0.4

Table 2. Fatty acid content (% total fatty acids) of marine and terrestrial primary producers, herbivores/omnivores, and carnivores (mean ± standard error). Different superscripts in the same column (i.e. for each fatty acid) indicates significant differences among trophic levels within each biome.

Trophic level	ALA	LNA	ARA	EPA	DHA	∑SFA	∑MUFA	∑PUFA	∑n-3 FA	∑n-6 FA	DHA/EPA
Marine											
Primary producers[1]	4.83 ± 0.8a	3.59 ± 0.2a	3.17 ± 0.2b	12.3 ± 0.4b	3.84 ± 0.2c	36.4 ± 0.6a	23.7 ± 0.4c	38.1 ± 0.6b	23.7 ± 0.4b	6.85 ± 0.3a	2.5 ± 0.3a
Herbivores/omnivores[2]	1.61 ± 0.1b	2.34 ± 0.2b	4.54 ± 0.2a	13.8 ± 0.3a	9.18 ± 0.3b	27.5 ± 0.4b	26.3 ± 0.4b	42.9 ± 0.5a	26.3 ± 0.5b	6.88 ± 0.3a	0.9 ± 0.1b
Carnivores[3]	0.67 ± 0.0b	1.37 ± 0.1c	2.09 ± 0.2c	8.18 ± 0.2c	15.4 ± 0.4a	25.1 ± 0.4c	37.8 ± 0.6a	34.4 ± 0.6c	38.1 ± 0.6a	3.45 ± 0.2b	2.2 ± 0.1a
Terrestrial											
Primary producers[1]	11.1 ± 0.8a	38.4 ± 1.0a	0.52 ± 0.1c	0.00 ± 0.0c	0.00 ± 0.0b	20.8 ± 0.8c	52.5 ± 2.1a	50.3 ± 1.0a	26.6 ± 0.9c	36.4 ± 1.5a	-
Herbivores/omnivores[2]	8.72 ± 0.5b	14.1 ± 0.5b	8.07 ± 0.8a	0.62 ± 0.1b	3.12 ± 0.2a	39.2 ± 0.7a	33.4 ± 0.7b	27.5 ± 0.7b	33.4 ± 0.7b	18.4 ± 0.7b	5.0 ± 0.2a
Carnivores[3]	6.92 ± 3.6c	7.87 ± 0.9c	2.35 ± 0.7b	2.39 ± 0.4a	3.25 ± 0.4a	25.4 ± 1.6b	26.6 ± 0.9c	20.6 ± 1.2c	52.5 ± 0.2a	10.2 ± 1.4c	1.6 ± 0.2b
Biome term (p-value)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.819	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Trophic term (p-value)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.009	< 0.001	< 0.001

[1]Primary producers: phytoplankton, macrophytes, and terrestrial plants
[2]Herbivores/omnivores: annelids, bivalves, certain crustaceans, echinoderms, zooplankton, terrestrial insects, and certain terrestrial mammals
[3]Carnivores: cephalopods, certain crustaceans, fish, marine mammals, and certain terrestrial mammals

Table 3. Fatty acid content (% total fatty acids) of marine organisms in three latitudinal zones: polar (90-60ºN and S), temperate (60-30ºN and S), and tropical (30ºN to 30ºS). Different superscripts, in the same column (i.e. for each fatty acid), indicate significant differences among latitudinal zones.

Latitudinal zone	ALA	LNA	ARA	EPA	DHA	∑SFA	∑MUFA	∑PUFA	∑n-3 FA	∑n-6 FA	DHA/EPA
Polar (n=372)	1.7 ± 0.2	2.1 ± 0.2	1.9 ± 0.3^{a}	13.6 ± 0.5^{a}	10.5 ± 0.4^{a}	22.2 ± 0.5^{a}	39.9 ± 0.9^{a}	42.8 ± 0.8^{a}	24.5 ± 0.7^{a}	4.1 ± 0.3^{a}	1.9 ± 0.2
Temperate (n=1217)	2.6 ± 0.4	2.6 ± 0.1	3.8 ± 0.1^{b}	12.3 ± 0.2^{b}	9.7 ± 0.3^{a}	30.1 ± 0.4^{b}	26.3 ± 0.4^{b}	40.1 ± 0.4^{b}	24.6 ± 0.6^{a}	6.4 ± 0.2^{b}	1.5 ± 0.1
Tropical (n=263)	2.3 ± 0.3	3.1 ± 0.2	4.6 ± 0.3^{c}	6.9 ± 0.4^{c}	8.3 ± 0.6^{b}	35.1 ± 0.8^{c}	26.3 ± 0.7^{b}	34.7 ± 0.8^{c}	18.1 ± 0.7^{b}	7.7 ± 0.4^{c}	2.5 ± 0.3

Table 4. Fatty acid content (% total fatty acid; mean ± standard error) in marine and terrestrial organisms, with results of ANOVA (model 2; biome and trophic level as categorical variables).

Fatty acid	**Marine**	**Terrestrial**	**Biome**		**Trophic level**	
			F-stat	p-value	F-stat	p-value
ALA	2.3 ± 0.3	9.6 ± 0.5	177	< 0.001	20.1	< 0.001
LNA	2.5 ± 0.1	23.6 ± 0.6	2121	< 0.001	272	< 0.001
ARA	3.4 ± 0.1	7.2 ± 0.6	52.2	< 0.001	37.1	< 0.001
EPA	11.7 ± 0.1	0.9 ± 0.1	405	< 0.001	71.5	< 0.001
DHA	9.2 ± 0.2	2.1 ± 0.1	167	< 0.001	329	< 0.001
∑SFA	29.8 ± 0.3	31.6 ± 0.6	0.05	0.819	48.6	< 0.001
∑MUFA	28.8 ± 0.3	31.8 ± 0.6	101	< 0.001	210	< 0.001
∑PUFA	38.9 ± 0.3	35.8 ± 0.7	43.3	< 0.001	86.5	< 0.001
∑n-3 FA	23.2 ± 0.4	6.3 ± 0.3	202	< 0.001	12.3	0.009
∑n-6 FA	5.7 ± 0.2	17.6 ± 0.7	482	< 0.001	53.2	< 0.001

[1]Sum of n-3 = ALA + EPA + DHA
[2]Sum of n-6 = LNA + ARA

Table 5. ANOVA models used to analyze fatty acid content (% total fatty acids) in marine and terrestrial organisms.

Model number	Model type	Variables	Objective
1	ANOVA	Biome (categorical) Taxonomic Group (categorical) Biome x Group Interaction	To determine the effect of biome, taxonomic group, and their interaction on fatty acid content in all organisms
2	ANOVA	Biome (categorical) Trophic level (categorical)	To determine if fatty acid content in organisms depends on increasing trophic level in either biome
3	ANOVA	Taxonomic group (categorical) Latitudinal zone (categorical)	To determine the effect of taxonomic group and latitudinal zone on the fatty acid content of marine organisms
4	ANOVA	Latitudinal zone (categorical) Trophic level (categorical)	To determine if fatty acid content in marine organisms depends on increasing trophic level among latitudinal zones
5	ANOVA (nested)	Trophic level (categorical) Taxonomic group (nested factor)	To determine whether trophic level or taxonomic group (within each trophic level) are more important in predicting FA content in marine organisms[1]
6	ANOVA (nested)	Taxonomic group (categorical) Latitudinal zone (nested factor)	To determine whether the fatty acid content in marine organisms differs depending on latitudinal zone within each taxonomic group

[1]In this model, we were not interested in the distinct taxonomic group, but rather the difference among random groups within each trophic level.

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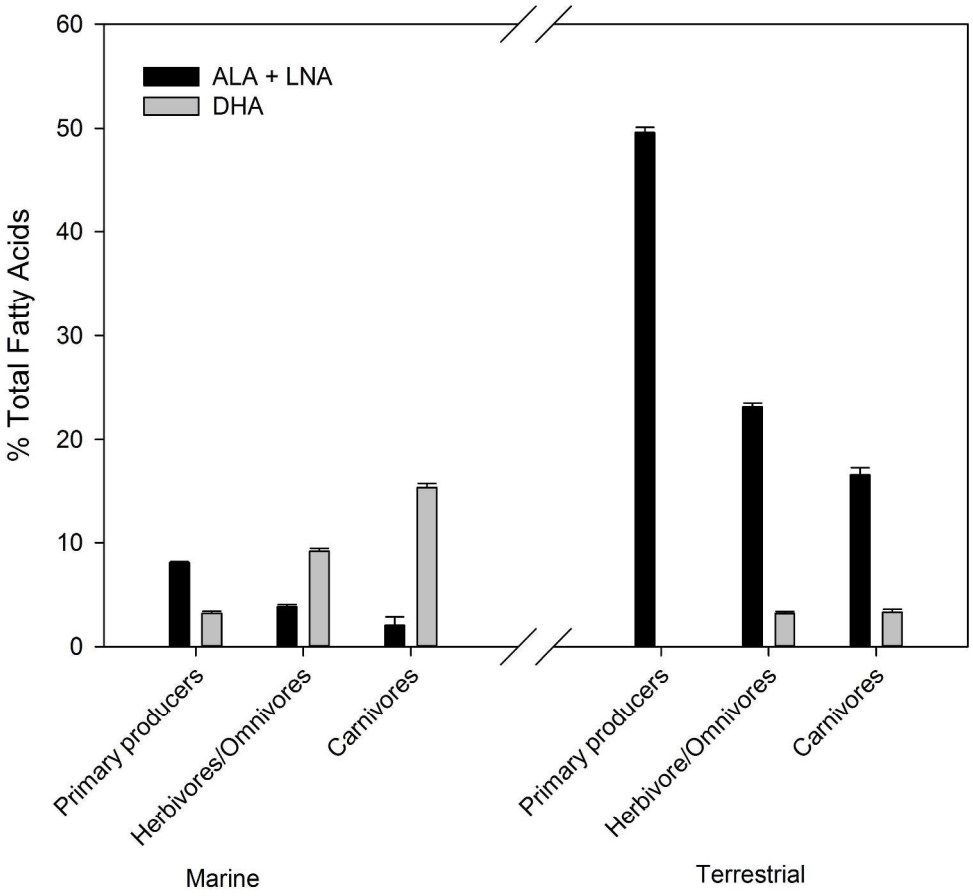

Fig. 1. Sum of ALA + LNA and DHA (mean ± SE) by trophic level in marine and terrestrial organisms.

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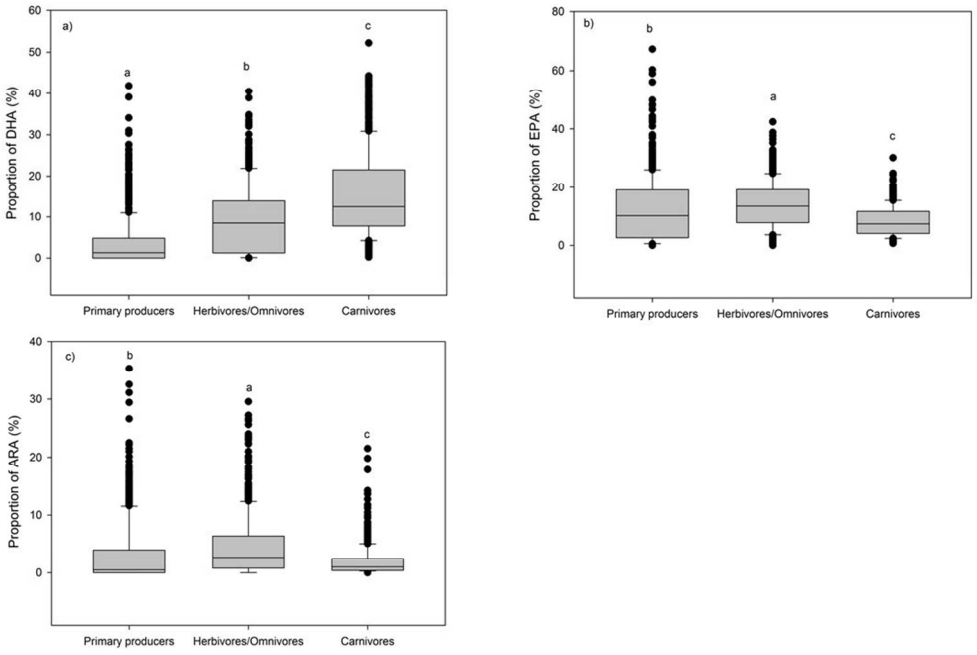

Fig. 2. Boxplots of a) DHA, b) EPA, and c) ARA levels in marine organisms by trophic level (primary producers to carnivores), where $p < 0.001$ and different superscripts indicate significant differences among trophic levels for each LC-PUFA.

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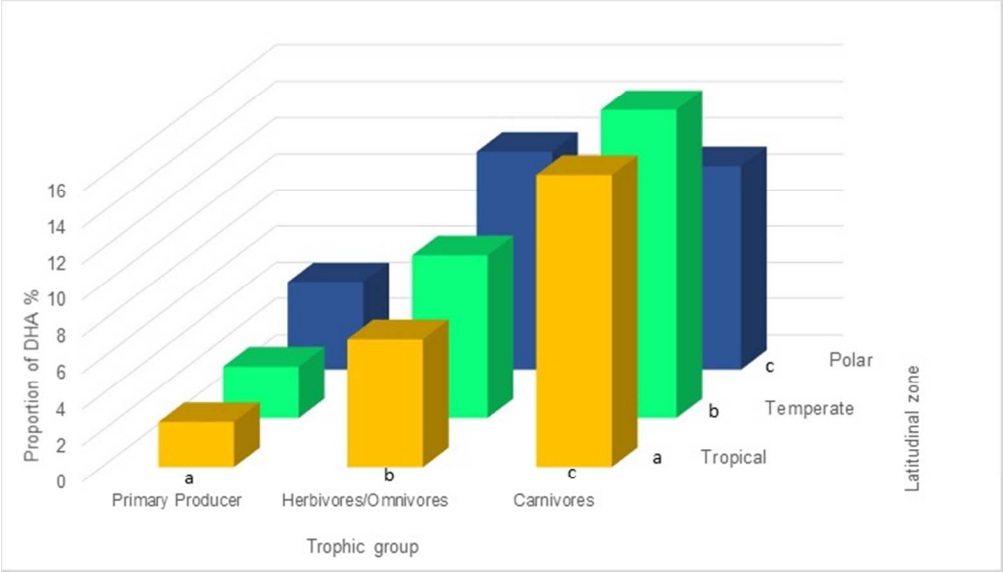

Fig. 3. Three-dimensional representation of DHA (%) in marine organisms organized by trophic level (x-axis) and latitudinal zone (z-axis). See Table S5 for mean values (± standard error) and Table S6 ANOVA model p-values. Different letters indicate significant differences among each factor, trophic level (applies to DHA in three trophic levels, regardless of latitudinal zone) and latitudinal zone (applies to DHA in three zones, regardless of trophic level).

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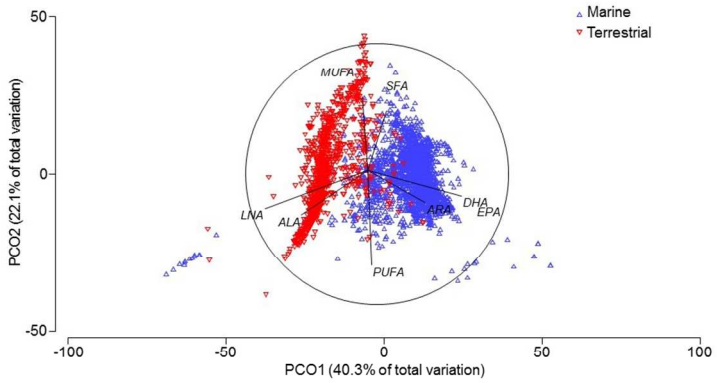

Fig. 4. Principal coordinates analysis plot of fatty acids in marine and terrestrial organisms (n=3,072), using a Bray-Curtis similarity matrix (square root transformed).

338x190mm (96 x 96 DPI)

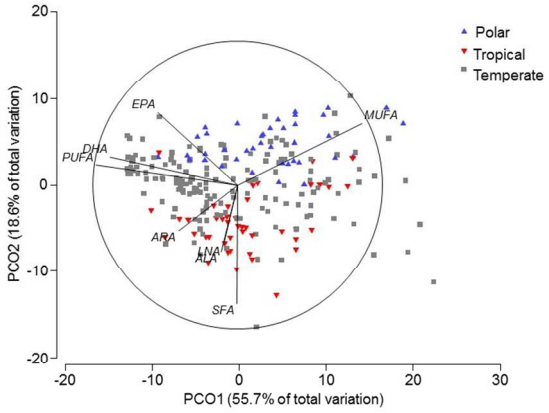

Fig. 5. Principal coordinates analysis of fatty acids in marine fish (n=239) by latitudinal zone, using a Bray-Curtis similarity matrix (square root transformed).

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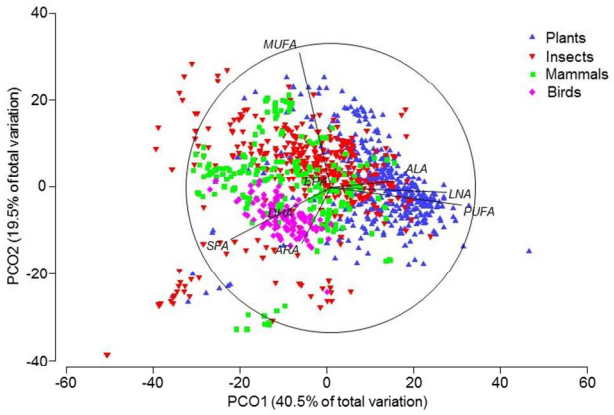

Fig. 6. Principal coordinates analysis of fatty acids in terrestrial organisms (n= 1,009) by taxonomic group, using a Bray-Curtis similarity matrix (square-root transformed).

338x190mm (96 x 96 DPI)