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Lipid dynamics in the southern hemisphere: a 30-year meta-analysis of marine consumers

Bowen Zhang[1,2,*], Heidi Pethybridge[2], Patti Virtue[1,2], Peter D. Nichols[1,2]

[1]Institute for Marine and Antarctic Studies, University of Tasmania, Battery Point, Tasmania 7004, Australia
[2]CSIRO Environment, Battery Point, Tasmania 7004, Australia

ABSTRACT: Assessing the total lipid content (TLC, expressed as % wet weight, WW) and constituent fatty acid (FA) composition (expressed as % of total FA) in marine organisms provides vital knowledge about the transfer of energy and essential nutrients from primary producers to higher-order consumers, including humans. To obtain a broad understanding of marine lipid dynamics, we used information from more than 470 species of Australian and Southern Ocean marine consumers spanning across the food web, from secondary to apex predators, sampled over a 30 yr period (1989 to 2019). Taxa group, trophic guild, and collection period were found to be the most influential drivers of variability in 4 key variables (TLC, docosahexaenoic acid [DHA, 22:6n-3], eicosapentaenoic acid [EPA, 20:5n-3] and arachidonic acid [ARA, 20:4n-6]). Highest TLC was observed in marine mammals and mid-trophic consumers, highest DHA occurred in fish and apex predators, highest EPA occurred in krill and other lower-level consumers, and highest ARA was present in rays and other apex predators. Horizontal habitat type was also an important driver with significantly higher TLC, EPA, and DHA found in samples from oceanic and pelagic habitat types, whilst coastal habitat samples had significantly higher ARA. Generalised additive mixed models determined that there were regional spatial patterns and interannual trends for all variables over the 30 yr period across all taxa groups. This study provides new understanding of the spatial distribution, temporal trends, and drivers of lipid and essential fatty acids (EFA) in marine ecosystems in the southern hemisphere.

KEY WORDS: Consumers · DHA · Ecosystem assessments · Environment · EPA · Fatty acids · Habitat · Marine ecosystem · Meta-analysis

1. INTRODUCTION

Lipids and their fatty acid (FA) constituents are nutrients that are essential to all forms of life because of their roles in membrane structure and biological processes such as energy transfer and metabolism (Dalsgaard et al. 2003, Parrish 2013). Measurements of total lipid (or fat) content (TLC) provide an understanding of how organisms and ecosystems function through the storage, transfer and use of energy over time and space (Falk-Petersen et al. 2000, Hagen et al. 2001). The recognized importance of wax esters in certain copepods and myctophid fish (Sargent & Falk Peterson 1981) can also be used in addition to TLC as an indicator of the nutritional condition of individuals (Tocher & Ghioni 1999, Falk-Petersen et al. 2000) or community-level productivity (Pethybridge et al. 2013). Profiling of FAs has proven useful qualitatively, and in some cases quantitatively, to describe dietary interactions, dominant basal source contributions, and habitat dependencies (Budge et al. 2007). In comparison to other biochemical tracers, such as stable carbon and nitrogen isotopes, FAs typically provide information on organism trophodynamics at finer taxonomic resolution and shorter time scales (Beckmann et al. 2013).

*Corresponding author: b.zhang@utas.edu.au

FAs are the building blocks of complex lipids and are biologically active substances with key biological functions, and serve as important nutrients for aquatic animals (Calder & Grimble 2002). FAs are grouped into several categories (Williams 2000): saturated fatty acids (SFA), monounsaturated fatty acids (MUFA) and polyunsaturated fatty acids (PUFA). Two well-known groups of PUFA are omega-3 (n-3 PUFA) and omega-6 (n-6 PUFA). Many consumers, including humans, cannot synthesise these FAs de-novo and must obtain them from their food, hence they are known as dietary essential nutrients. Omega-3 long-chain (LC, ≥C20) PUFA (n-3 LC-PUFA) refers to FA with a chain length of twenty or more carbon atoms and 2 or more double bonds. The 2 most important omega-3 LC-PUFA are eicosapentaenoic acid (EPA; 20:5n-3) and docosahexaenoic acid (DHA; 22:6n-3), which are abundant in marine environments as they are synthesised by phytoplankton (Swanson et al. 2012). EPA and the n-6 LC-PUFA arachidonic acid (ARA; 20:4n-6) are synthesised by large phytoplankton such as diatoms, various macroalgae (Schmid et al. 2018) and also selected heterotrophs (Lee Chang et al. 2011, 2013, 2014), while DHA is synthesised by smaller phytoplankton such as flagellates (Dalsgaard et al. 2003, Parrish 2009, 2013). The formation of polyunsaturated fatty acids (PUFAs) is restricted to only a few organisms, with phytoplankton being the most notable source. The availability of n-3 LC-PUFA, in both fish and humans, is primarily dependent on dietary intake and the capacity to extend and modify plant-derived alpha-linolenic acid (ALA) into their longer C20 and C22 counterparts, in particular EPA and DHA (Tocher & Ghioni 1999, Bergé & Barnathan 2005). This conversion of shorter chain n-3 PUFA to n-3 LC-PUFA is generally limited for most marine species, and ultimately also for human consumers. ARA plays an important role in reproduction (Becker & Boersma 2005), although it is considered to be of lower nutritional value (relative to the n-3 LC-PUFA) to top predators, including humans, and is thought to be largely derived from benthic or coastal primary producers (Hartwich et al. 2012, Marzetz et al. 2017).

In marine organisms, there are typically only around 20 FAs that are detected at relative levels of higher than 1% (Parrish et al. 2015, Pethybridge et al. 2015), although there are large differences between species profiles due to various abiotic and biotic factors. At the organism level, there are large differences in the lipid and FA composition of different tissue types (Nichols et al. 1998, Dalsgaard et al. 2003, Gladyshev et al. 2018), with higher TLC and MUFA thought to occur in storage tissues (e.g. liver, blubber, stomach) and higher PUFA generally found in structural tissues (e.g. muscle). At the higher levels of organisms, regional studies have reported distinct differences in TLC and FA composition due to taxa group (Nichols et al. 1998, Budge et al. 2002, Phleger et al. 2002, Pethybridge et al. 2010, Gladyshev et al. 2018, Meyer et al. 2019), habitat (Dunstan et al. 1988, Parrish et al. 2005, Meyer et al. 2019), climate or environmental zone (Nanton & Castell 1999, Litzow et al. 2006), and temperature (Hixson et al. 2015, Pethybridge et al. 2015). In a global meta-analysis of EPA and DHA (expressed as a percentage of total FA composition) levels in 173 fish species, Gladyshev et al. (2018) showed that phylogenetic and ecomorphological (e.g. habitat type and feeding mode factors) explained the greatest variation between species. In another global meta-analysis, Meyer et al. (2019) identified certain FAs in the muscle of chondrichthyan species that were directly related to habitat type, trophic guild, phylogeny and temperature zones. In general, these studies suggest that the highest levels of TLC and n-3 LC-PUFA can be found in particular orders (such as Clupeiformes or Salmoniformes fish) and species from colder and more productive marine habitats. Visser et al. (2020) however, found that season is an important factor in TLC level.

In this study we performed a meta-analysis of lipid and FA data derived from a diverse range of consumers, from secondary to apex predators, sampled in Australian, Indian Ocean and Southern Ocean waters over a 30 yr period. The marine area includes highly diverse environments and climate zones comprising offshore and sub-Antarctic islands that consist of a variety of ecosystem and habitat types — coastal, continental shelf, oceanic, and ranging from tropical to sub-Antarctic. The wide range of taxa and environmental conditions, along with the latitudinal and longitudinal spread, provided for a forward-looking case study to (1) better understand the spatial and temporal distribution and availability of these essential nutrients, and (2) gain insights into the main abiotic and biotic drivers of such patterns and trends and how they might be impacted by environmental change. Such information is critical for enhancing our understanding of marine ecosystem functions and services for different climate zones and it will also improve assessments of the dietary composition and habitat utilization of marine consumers, which is key to effective ecosystem-based resource management.

2. MATERIALS AND METHODS

2.1. Data collection and compilation

We used a compiled data set that consisted of 4856 records from 521 species sampled over a 30 yr period (from 1989 to 2019) around Australian and Pacific, Indian and Southern Ocean waters (Nichols et al. 2023) (Fig. 1). Each record had information, where available, on the length, weight, tissue type, mean trophic position, sampling date, vertical and horizontal habitat type, taxonomy, and geographic location and environment (based on latitude and longitude coordinates) of the individual (summarised in Nichols et al. 2023). The most records for any given species were from albacore tuna *Thunnus alalunga* (n = 478), Antarctic krill *Euphausia superba* (n = 465), spurdog sharks *Squalus acanthias* (n = 364), humpback whales *Megaptera novaeangliae* (n = 335), and white sharks *Carcharodon carcharias* (n = 277). Another 4 species had >100 records (Weddell seal *Leptonychotes weddellii*, New Zealand fur seal *Arctocephalus forsteri*, arrow squid *Nototodarus gouldi*, and whale shark *Rhincodon typus*).

2.2. Analytical methods

Methods employed across the numerous studies performed at the CSIRO Marine Laboratories in Hobart from which the data in this study originate have been described in detail elsewhere (Parrish et al. 2015, Nichols et al. 2023). Briefly, samples were extracted using the modified traditional Bligh and Dyer protocol (Bligh & Dyer 1959), and aliquots of the total lipids were then methylated and analysed by gas chromatography (GC) and GC-mass spectrometry. Total lipid content (expressed on a percent wet weight [%WW] basis) was determined gravimetrically. Relative individual FA composition is the percentage composition of the total fatty acid profile (termed %TFA) of the sample. Samples used were either individual specimens or an average of replicate specimens.

2.3. Statistical analysis

For the statistical analysis, the month of sampling was used to broadly classify the season into either winter (April–September) or summer (October–March). Taxa groups that had sampling sizes lower than 20 were not included in statistical tests or models, and krill is separated from zooplankton because of the large number of records that could have skewed the data for broader groups. To explore the effect of trophic position, we used 3 different levels (2–3, 3–4, >4) to classify trophic guild (into lower, mid and higher level consumers). Year was also converted to a nominal category variable to investigate potential broad temporal level differences with 5 yr and 10 yr periods. Body size (total length; cm) effects were categorized into 3 levels (small: <10 cm; medium: 10–50 cm; large: >50 cm). The length data were obtained from the original research and online information systems including FishBase and Sealifebase (https://www.fishbase.se and https://www.

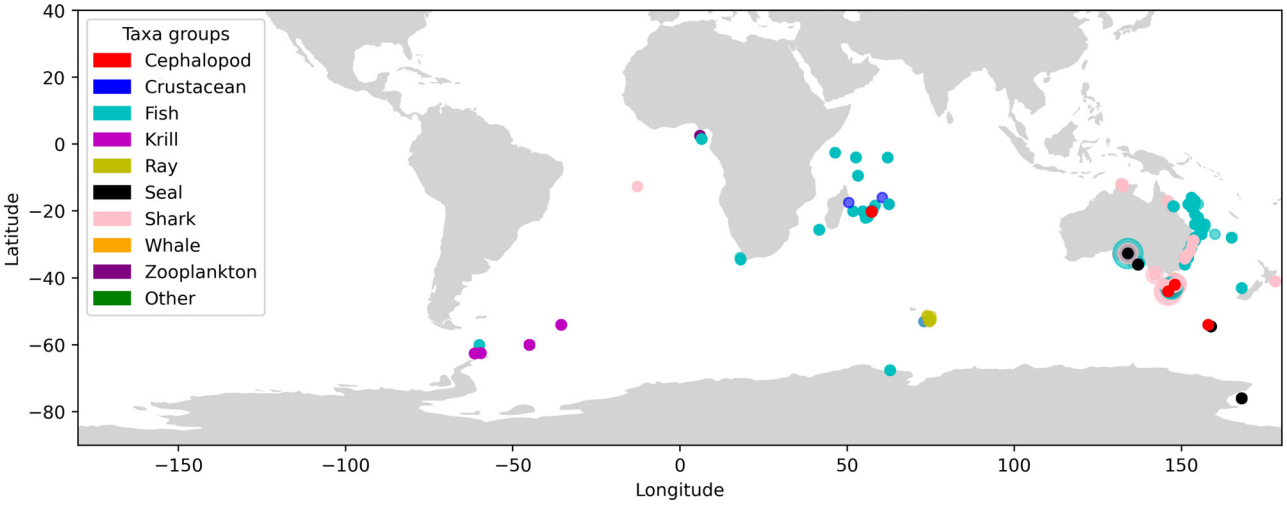

Fig. 1. Sample locations of all taxa groups (with n < 20 named as 'Other') from the southern hemisphere. Sample-size is indicated by dot size

sealifebase.ca, accessed February 2023), and taxa groups of organisms were also considered for categorization purposes.

One-way analysis of variance (ANOVA) and 2-way ANOVA tests (Dong & Wedel 2017) were used to test the single and interaction factors of tissue type, taxa group, season, environment, habitat type, year, size and trophic guild on TLC (%WW), and the FA variables (all measured as % TFA, expressed as area %). The Bonferroni correction was employed to adjust the p-values for multiple comparisons, and *F*-values were used to determine the amount of explained variance, with the best models having the largest values. A factor was determined to be statistically significant if p-values were less than 0.001. Post-hoc Tukey HSD tests were used to explore within-factor differences in means while boxplots were used to visualize differences, patterns, and trends, and the significance value (alpha) was set to 0.05.

Generalized additive mixed models (GAMMs) (Wood 2006) were developed to examine non-linear and temporal (year) and spatial (longitude, latitude and interaction) trends and patterns of the 4 key lipid variables across all taxa, tissues and habitat types. Before constructing GAMMs, the assumptions including normality, variance, homogeneity of variances, and collinearity were tested using methods through calculating leverage, residual analysis and Bartlett's test. We also checked the normal Q–Q and residual versus fitted values plots. GAMMs were then constructed from gamm4 package in R with a negative binomial distribution (Zuur et al. 2009a). To test negative binomial model assumption of variance and independence, diagnostic plots and other summarised methods were tested (Wood 2006). Data transformations were deemed unnecessary to perform the models. Taxa group was incorporated as a random factor to account for overdispersal and intragroup correlations (Zuur et al. 2009b). The degree of smoothing (the *k* parameter) in the models was restricted according to factor flexibility to avoid overfitting. All marginal terms in the model were examined using smoothing splines, while geographic covariates were modelled by a scale-invariant tensor product. Separate models were built for each predictor to investigate how much variation was explained by the particular predictors. The standard diagnostics, including Akaike's Information Criterion (AICc) and percent deviance explained (%DE and pseudo R^2), were reported and used to check model performance (Wood 2006). To test for consistency in temporal trends, we undertook separate GAMMs for fish, sharks, and krill. To visualise large-scale spatial patterns, contour maps were produced based on outputs of GAMMs for geographic location (latitude and longitude). All performed data analyses were conducted using R software, v.3.2.3 (R Core Team 2009).

3. RESULTS

ANOVA results showed that the 3 single variables that most explained variability in all 4 tested lipid variables were taxa group, trophic guild and year of sampling (Table 1). Tissue type, environment, and horizontal habitat type also significantly influenced all lipid variables ($p < 0.001$), but *F*-values were lower suggesting reduced variability between group means relative to the within-group variability. Vertical habitat type was significant for all FA variables (DHA, EPA and ARA) but not TLC, while season was only significant for DHA and EPA. The boxplots demonstrated high variability and some clear differences among factor levels (Fig. 2).

3.1. Biotic drivers

A 1-way ANOVA revealed that taxa type, trophic guild, tissue type and body size significantly influenced all the variables tested (Table 1) with differences observed between factor levels (Fig. 2). Marine mammals, especially whales, had higher TLC compared to all other taxa, with mean differences of >40% occurring between whale and zooplankton (Tukey HSD test). Crustaceans and fish were highest in DHA whilst whales and seals had the lowest levels. For EPA, the highest levels were found in krill and zooplankton while the lowest levels were in marine mammals and sharks. Sharks and rays had the greatest ARA levels, whereas krill and marine mammals had the lowest (Fig. 2a). There were significant differences found between the 3 different trophic guilds for all lipid and FA variables tested (Table 1). A noticeable trend was observed for EPA, which declined in moving from lower to higher order consumers, while ARA showed an increasing trend, although not across all taxa groups (Fig. 2b). Structural tissues and selected fish had the highest proportions of ARA (10–16%TFA) at the mid trophic level. EPA exhibited the highest levels in phytoplankton, especially diatoms, and from there it is transferred through trophic levels, declining or fading away moving up the food chain. The Tukey HSD tests indicated that mid-trophic consumers had the largest dif-

Table 1. Summary of ANOVA test results for total lipid content (TLC; % wet wt), docosahexaenoic acid (DHA; %), eicosapentaenoic acid (EPA; %), and arachidonic acid (ARA; %) (all FA data are expressed as a percentage of total FA composition) to test the single effects of the main independent factors (vertical habitat; horizontal habitat; environment or climate zones; season; taxa groups; tissue types; category trophic position; category year; longitude; latitude) and interactive effects (only $p < 0.001$ were listed) examined in this study. Non-significant factors' p-values are italicised. For single taxa group factor, only $n > 20$ is examined to minimize the effect of size. df: degrees of freedom (between and within-group df values separated by comma)

	TLC				DHA			EPA			ARA		
	df	MS	*F*	Pr(>*F*)	df	MS	*F*	Pr(>*F*)	df	MS	*F*	Pr(>*F*)	df	MS	*F*	Pr(>*F*)	df	MS	*F*	Pr(>*F*)
Taxa groups	9, 1917	49934	308.69	<0.001	14, 4840	12524	1030.1	<0.001	14, 4841	6927	2207.76	<0.001	14, 4505	2396.5	571.42	<0.001
Environment	3, 1912	8184	18.96	<0.001	3, 4840	16766	79.06	<0.001	3, 4841	12379	7.65	<0.001	3, 4505	5671	205.7	<0.001
Tissue	3, 1923	70315	32.38	<0.001	3, 4851	14344	13.74	<0.001	3, 4852	6537	13.51	<0.001	3, 4516	10553	37.75	<0.001
Vertical habitat	2, 1902	12586	0.8	*0.37*	2, 4829	15658	44.78	<0.001	2, 4830	6592	15.38	<0.001	2, 4494	3520	256.22	<0.001
Horizontal habitat	3, 1914	10445	33.96	<0.001	3, 4842	8093	84.23	<0.001	3, 4843	6062	23.02	<0.001	3, 4507	8473	149.13	<0.001
Season	1, 1240	45.14	0.03	*0.69*	1, 3285	408	50.29	*0.05*	1, 3285	113.78	29.55	*0.09*	1, 2983	1145.2	0.26	*0.61*
Size (big; medium; small)	3, 1923	12197	63.54	<0.001	3, 4851	3317	73.22	<0.001	3, 4852	7128	1586	<0.001	3, 4516	2612	127	<0.001
Trophic guild	2, 1428	66255	370.4	<0.001	2, 3411	11739	258	<0.001	2, 3411	37835	1786.33	<0.001	2, 3106	3355	257.9	<0.001
Time period (5 yr)	4, 1922	18860	29.03	<0.001	5, 4770	10709	129.5	<0.001	5, 4770	2196.8	81.27	<0.001	5, 4434	2151.9	82	<0.001
Time period (10 yr)	2, 1924	31631	114.5	<0.001	2, 4773	6536	73	<0.001	2, 4773	3982	221.33	<0.001	2, 4437	4586	242.4	<0.001
Taxa groups: Environment	22, 1893	21361	125.02	<0.001	36, 4807	6528	356.02	<0.001	36, 4808	2912.8	922.67	<0.001	36, 4472	1330.6	387.25	<0.001
Taxa groups: Tissue	18, 1908	29820	42.98	<0.001	29, 4825	7219	18.15	<0.001	29, 4826	3433	14.09	<0.001	29, 4490	1557.8	39.5	<0.001
Taxa groups: Habitat_vertical	17, 1887	26695	0.39	*0.53*	27, 4804	7367	60.18	<0.001	27, 4805	3613	13.78	<0.001	27, 4469	1968.2	434.34	<0.001
Taxa groups: Habitat_horizontal	21, 1896	22081	123.41	<0.001	32, 4813	6983	27.2	<0.001	32, 4814	3184	12.49	<0.001	32, 4478	1641.2	16.38	<0.001
Taxa groups: Time period (10 yr)	19, 1907	24992	166	<0.001	28, 4747	7196	141	<0.001	28, 4747	3657	381.9	<0.001	28, 4411	1382.4	122.9	<0.001
Taxa groups: Trophic guild	7, 1423	53594	216.2	<0.001	9, 3404	18381	196.6	<0.001	9, 3404	8963	514	<0.001	9, 3099	3374	180.2	<0.001
Size:Taxa groups	23, 1903	20402	134.2	<0.001	41, 4813	4852	119.1	<0.001	41, 4814	2452.4	317.5	<0.001	41, 4478	916.7	92.86	<0.001

ference with lower order consumers in TLC, EPA, and ARA, with differences from 32, 12 and 5%, respectively. The most significant difference in DHA was observed between mid-trophic and higher order consumers, with the latter group having 6% higher levels of DHA. Looking at the effect of tissue type, tissues serving fat storage, buoyancy and digestive roles (such as blubber, stomach, and liver) were higher in TLC and total EPA, while tissues serving a structural role (such as muscle) were low in TLC and high in DHA and ARA (Fig. 2c). There were significantly lower levels of DHA in storage tissue compared with structural (–6% difference) and reproductive (–4%) tissues, and EPA showed the opposite trend: highest variability in storage tissue, and lowest in structural and reproductive tissues (Fig. 2c). The highest relative level of ARA was generally observed in the structural tissue samples.

3.2. Abiotic drivers

Three categorical variables — environment, horizontal and vertical habitat type, each of which was significant for all 4 lipid variables — were tested by ANOVA to examine potential drivers of broad spatial variation (Table 1). Season was not a significant factor for any of the lipid variables. The categorical year variables (testing differences between nominal intervals of 5 and 10 yr) were highly significant ($p < 0.001$) for all 4 lipid variables, with high *F*-values indicating large differences between group means (Table 1, Fig. 2). Tukey post-hoc comparisons showed that there were few identifiable 5 yr trends for any of the lipid variables, though there were some decadal trends with statistical differences in TLC, DHA and EPA between samples collected in the first 10 yr (1989–1999) compared to those sampled in the second (1999–2009) and third (2009–2019) decades. The largest differences between the first

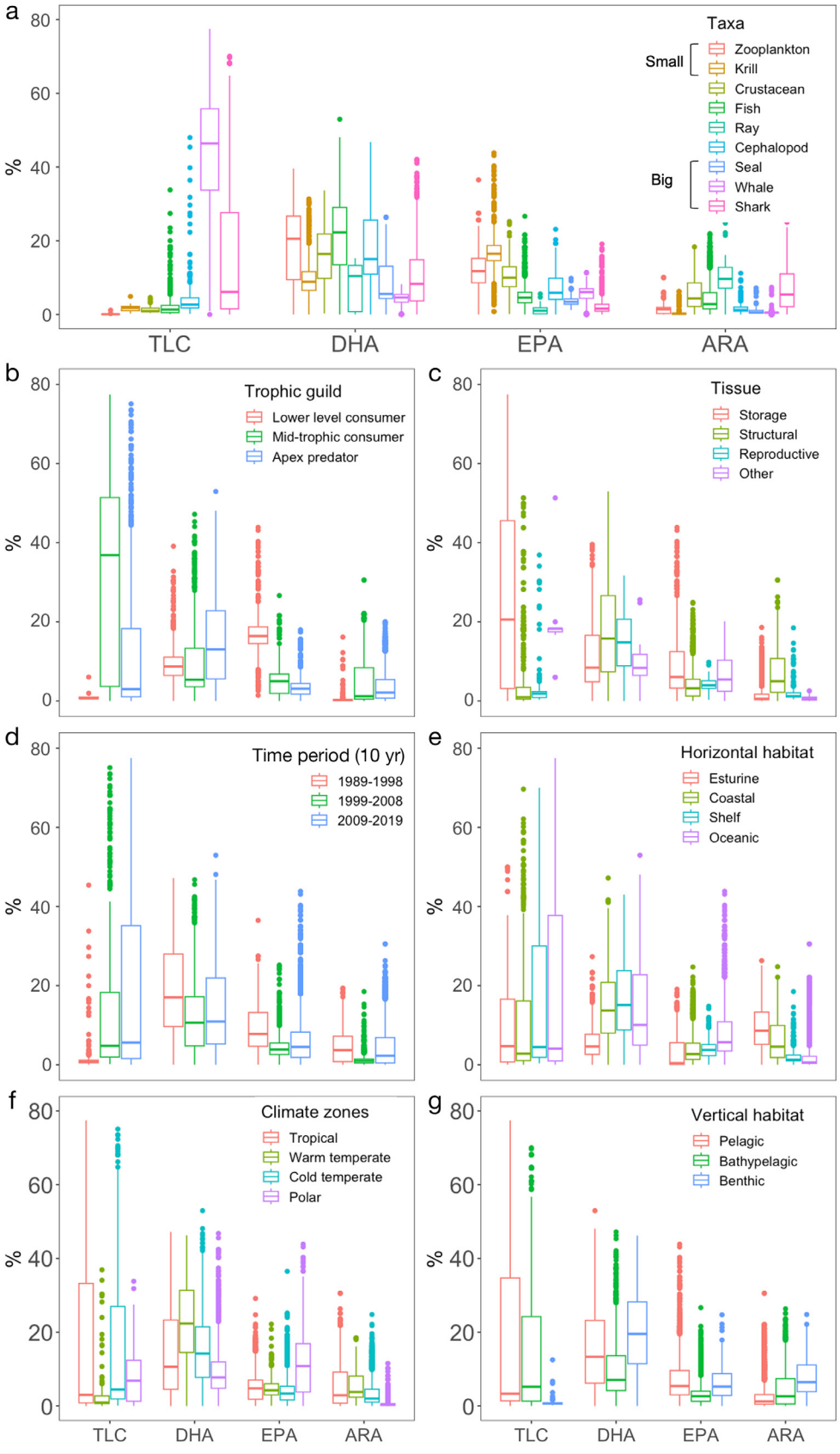

Fig. 2. Total lipid content (TLC; % wet wt), docosahexaenoic acid (DHA; %), eicosapentaenoic acid (EPA; %), and arachidonic acid (ARA; %) (all FA data are expressed as a percentage of total FA composition) under different conditions: (a) taxa groups, (b) trophic guild, (c) tissue types, (d) year with 10 yr as interval, (e) horizontal habitat, (f) environment or climate zones, (g) vertical habitat. Bars: means; boxes: standard deviations; whiskers: 95% confidence intervals; points: outliers

decade and the second decade were observed for DHA, EPA, and ARA, with differences of 6, 5, and 3%, respectively. However, for TLC, the highest lipid contents were detected in the third decade, showing a 16% increase compared to the first decade. TLC and EPA were statistically higher in samples obtained from polar environments, while DHA and ARA were higher in samples from temperate zones (Fig. 2f). With respect to horizontal habitat differences, oceanic habitats were characterized by high levels of TLC, moderate levels of DHA and EPA while low in ARA. There was an increasing trend of EPA and decreasing trend in ARA with distance from the coast, from estuarine to oceanic (Fig. 2e). Vertical habitat did not significantly explain variability in TLC, but did for all the FA variables. Benthic samples were significantly lower in TLC, and significantly higher in DHA and ARA. Bathypelagic systems had lower EPA while pelagic systems had low ARA (Fig. 2g).

3.4. Interaction effects

We used 2-way ANOVAs to test the influence of 2 categorical variables that had significant single variable effects (Table 1). Interactions with the higher *F*-values included taxa group and environment for DHA and EPA, taxa group and vertical habitat for ARA, and taxa group and TP for TLC. Post-hoc analyses of the interaction between taxa group and year (10 yr nominal categories) revealed significant differences between decadal time periods. Fish showed significant differences between the first and second, and between the second and third decade for all 4 variables, while there were also differences between the first and third decade for EPA. Sharks showed similar trends for TLC. Krill DHA and EPA significantly differed between the second and third decade and the first and third decade, respectively. Cephalopods had EPA levels that were statistically different between the first and third decade while crustaceans had statistically different ARA levels between the first and second decade. Samples from oceanic habitat types also showed significant differences between each of the 3 decades for all the lipid variables.

3.5. Temporal and spatial patterns and trends

Results from the GAMMs indicated that whilst most predictor variables were significant, longitude or latitude were better stand-alone explanatory variables than year for all 4 lipid variables tested (Table 2). The GAMM outputs showed that year alone explained 45, 54, 67 and 85% of the variation for DHA, EPA, ARA and TLC, respectively, across all taxa and tissue types. Over the 30 yr study period there was high interannual variability for all variables (Fig. 3). For TLC, levels increased around 1995–2003 and then again in 2015–2018. For DHA, relative levels seemed to have slightly increased in 1998 before declining in 2011. An opposite trend seems true for EPA, while ARA showed a clearer decline from 1990 to 2000 before marginally increasing from 2008. Using 10 yr as an interval, TLC showed a slight increase in trend while the 3 FA (DHA, EPA and ARA) had the lowest level in the second decade from 1999 to 2008 (Fig. 2d). The very broad temporal trends were comparable with the taxa specific predictions for fish, shark and krill (data not shown).

Regional gradients were visible on global contour maps for each of the 4 lipid variables across all species (Fig. 4). TLC was slightly higher in temperate zones and in the Atlantic Ocean and west Pacific Ocean. DHA and ARA were highest, while EPA was lowest in the Indian Ocean; however, latitudinal trends were not clear.

4. DISCUSSION

Lipid and FA analyses are being increasingly used to study the trophic ecology of consumers and marine ecosystem dynamics. While there are other lipid meta-analysis studies based on specific taxonomic groups (Meyer et al. 2019) and particular geographic regions (Pethybridge et al. 2018), there remain many gaps in our knowledge of the core biological and non-biological drivers of complex lipid dynamics. This study, through a broad community-level approach including lower, mid and higher level consumers, sought to provide further insights into large-scale drivers of spatial and temporal trends and patterns in marine lipids. Our study found that essential FA were significantly influenced by taxonomic group, trophic guild, collection period, tissue type, habitat type, and climate zone including at times complex interaction effects among these variables. Here we discuss each of these factors separately and relate our findings to prior research and theoretical understanding.

Table 2. Comparable performance of 6 generalized additive mixed models tested for total lipid content (TLC; % wet wt), docosahexaenoic acid (DHA; %), eicosapentaenoic acid (EPA; %), and arachidonic acid (ARA; %) (all FA data are expressed as a percentage of total FA composition), with the best model in **bold**. ΔAIC_c: difference in model Akaike information criterion for small sample sizes value relative to model with lowest AICc. %DE: percent deviance explained. *K*: number of parameters in the model. The degree of smoothing (the *k* parameter) is different for factors, with $k = 4$ for year and $k = 5$ for longitude and latitude

		Model	*K*	ΔAIC_c	%DE	p-value	R^2
TLC	1	Taxa_group	3	4986.08			
	2	*s*(Year) $k = 4$	5	4768.97	84.52	<0.001	0.03
	3	*s*(Longitude) $k = 5$	5	52.15	89.20	<0.001	0.11
	4	*s*(Latitude) $k = 5$	5	275.14	88.10	<0.001	0.01
	5	*t*(Longitude, Latitude)	9	39.92	89.47	0.020	0.07
	6	***s*(Year) + *t*(Longitude, Latitude)**	11	0.00	89.99		**0.02**
DHA	1	Taxa_group	3	10588.90			
	2	*s*(Year) $k = 4$	5	9992.77	45.15	0.040	0.00
	3	*s*(Longitude) $k = 5$	5	747.89	62.03	0.010	0.02
	4	*s*(Latitude) $k = 5$	5	874.51	67.89	<0.001	0.18
	5	*t*(Longitude, Latitude)	9	513.16	70.84	<0.001	0.23
	6	***s*(Year) + *t*(Longitude, Latitude)**	11	0.00	71.99		0.26
EPA	1	Taxa_group	3	8642.47			
	2	*s*(Year) $k = 4$	5	8251.51	53.74	<0.001	0.05
	3	*s*(Longitude) $k = 5$	5	290.18	63.65	0.000	0.36
	4	*s*(Latitude) $k = 5$	5	600.70	62.84	0.020	0.04
	5	*t*(Longitude, Latitude)	9	266.01	65.04	0.000	0.51
	6	***s*(Year) + *t*(Longitude, Latitude)**	11	0.00	66.25		0.39
ARA	1	Taxa_group	3	7232.35			
	2	*s*(Year) $k = 4$	5	6491.77	67.38	<0.001	0.07
	3	*s*(Longitude) $k = 5$	5	883.64	78.07	<0.001	0.16
	4	*s*(Latitude) $k = 5$	5	749	80.99	<0.001	0.22
	5	*t*(Longitude, Latitude)	9	527.03	84.63	<0.001	0.41
	6	***s*(Year) + *t*(Longitude, Latitude)**	11	0	85.89		0.54

4.1. Strong influence of taxa groups and trophic levels

This study found that taxa and trophic guild significantly influenced the TLC and FA compositions of marine organisms, similar to that shown in other meta-analysis and inter-comparison studies (Budge et al. 2002, Pethybridge et al. 2010, Gladyshev et al. 2018, Meyer et al. 2019). The tested FA parameters varied by up to 6 orders of magnitude (from 0.006 to 96.9% TFA composition) across the taxa groups, which is higher than those previously reported. For example, Gladyshev et al. (2018) assessed the muscle lipid and FA composition of 172 marine species belonging to 6 orders, and found that EPA and DHA levels varied within 2 orders of magnitude. For fish, Nichols et al. (1988) found that the level of PUFA ranged from 8 to 67%, which is similar to the results for fish in this study (1.2 to 66.5%). The slightly higher range of values across all the taxa observed in this study is likely due to the greater range of taxa and tissue types assessed. Taxa differences in TLC and dietary essential FAs reflect key differences in diet composition and trophic position (Iverson et al. 2004). Similar to other studies, our study found that fish have higher levels of n-3 LC-PUFA, including DHA and EPA, than crustaceans such as prawns (Cook et al. 2000, Kharlamenko et al. 2015, Gladyshev et al. 2018). We also found that large vertebrates had significantly higher TLC and total MUFA than other taxa, while fish had the highest levels of DHA and invertebrates had the highest levels of total PUFA and EPA. Conversely, krill contain high levels of EPA in particular and DHA (Virtue et al. 1995), and along with other crustaceans have been recognised as having higher PUFA than fish and squid (Pethybridge et al. 2010). This study found that levels of total MUFA increased with increasing trophic guild, while levels of total PUFA (and particularly EPA) decreased. EPA is derived from diatoms and it is a strong marker of diatom-based food webs (Dalsgaard et al. 2003, Parrish 2009, 2013), hence it is not surprising that the levels are highest in primary consumers that feed on diatoms, such as krill (Phleger et al. 2002, Hagen et al. 2007). Another example is MUFA such as 18:1n-9, which is a prominent indicator of carnivory, particu-

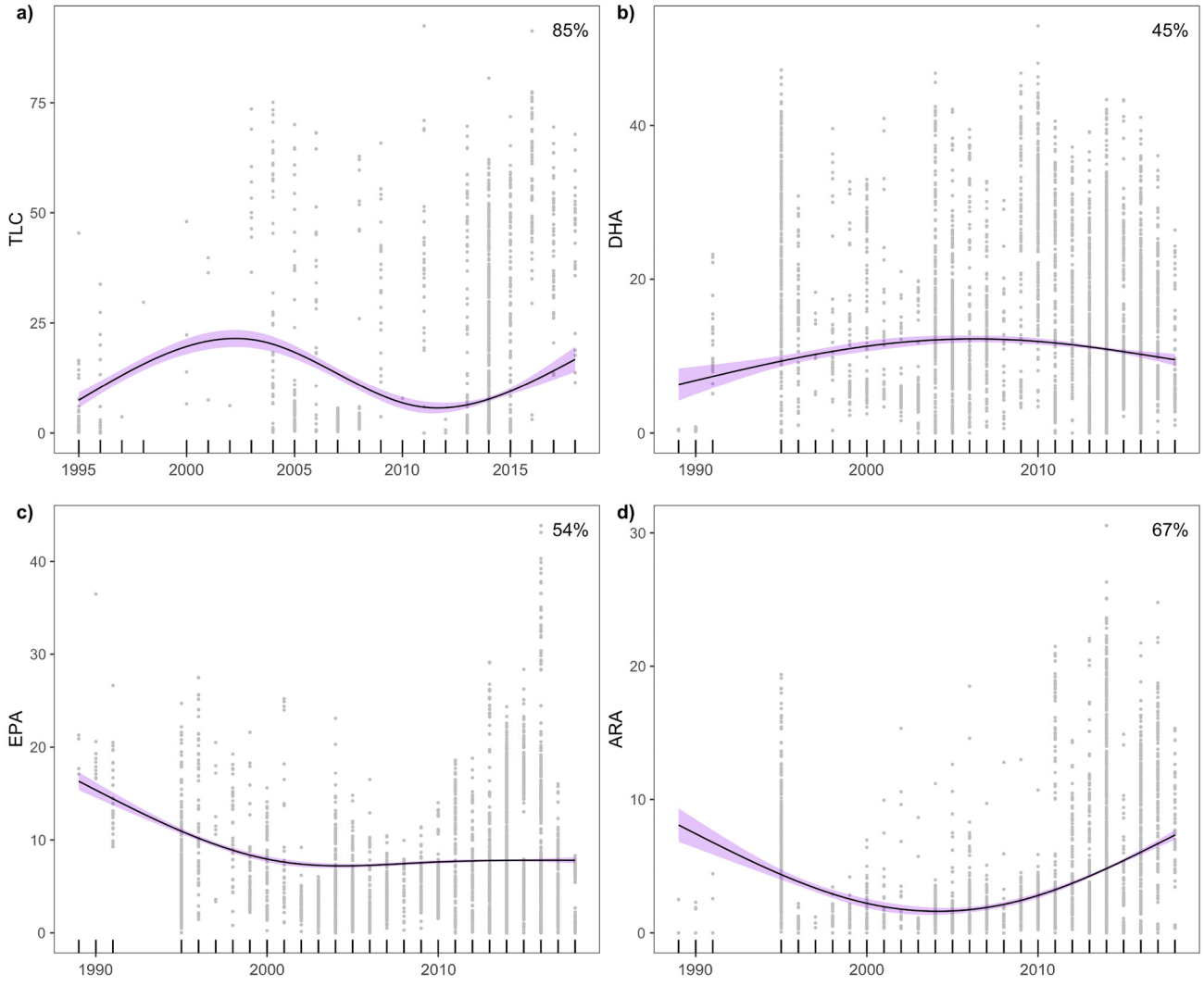

Fig. 3. Relationships between (a) total lipid content (TLC; % wet wt), (b) docosahexaenoic acid (DHA; %), (c) eicosapentaenoic acid (EPA; %) and (d) arachidonic acid (ARA; %) (all FA data are expressed as a percentage of total FA composition) with year from the generalized additive mixed model prediction and observations. Grey dots represent observed measures. The solid purple area shows the confidence limit of the models. The percent deviance explained from each variable is reported on the top right of each plot

larly in carnivores feeding higher in the food chain (Phillips et al. 2001, El-Sabaawi et al. 2009, Meyer et al. 2019).

4.2. Habitat affinity

As an organism's habitat strongly determines what nutrients it can access and how it interacts with other species, it is not surprising that in this study both vertical and horizontal habitat types explained a high degree of variation in FA profiles among different taxa. Specifically, this study found that higher TLC and total PUFA occurred in more productive (coastal and pelagic) habitats. Measurements of TLC have often been used as a tool to evaluate the energetic potential, or productivity, of a region (Parrish 2013), with 2 studies of Australian squid showing a strong correlation between digestive gland TLC (as %WW) and sea surface chl *a* concentrations (Phillips et al. 2002, Pethybridge et al. 2013). In the present study, samples derived from pelagic environments showed a mean TLC of 22.4 %WW, which is slightly higher than determined in previous studies (e.g. 6 to 18 % in Lea et al. 2002); this is likely due to the greater number of samples and also due to the inclusion of a larger number of records for fat storage tissues of large vertebrates. Several FA variables, including the SFA, PUFA, DHA, EPA, 16:0, 18:0 and ARA have been found to be useful indicators to characterize

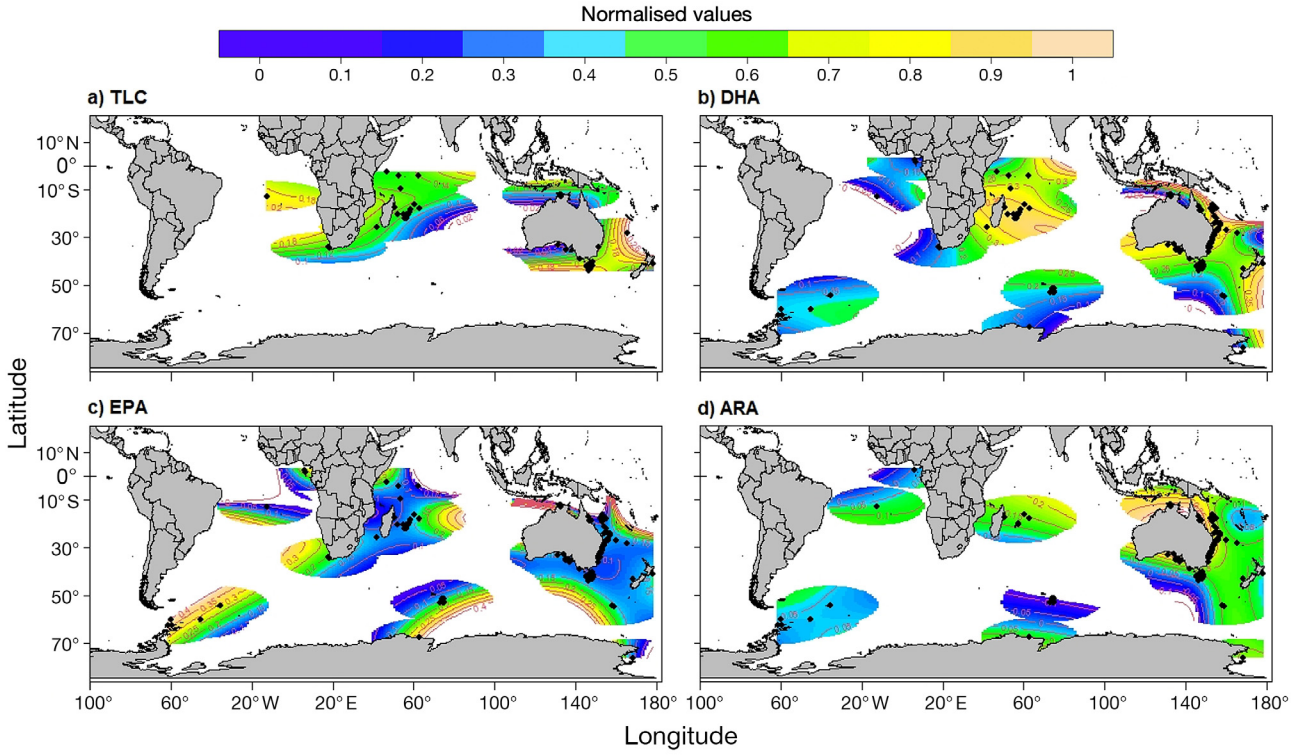

Fig. 4. Maps from the generalized additive mixed model of normalised values for (a) total lipid content (TLC; % wet wt), (b) docosahexaenoic acid (DHA; %), (c) eicosapentaenoic acid (EPA; %) and (d) arachidonic acid (ARA; %) (all FA data is expressed as a percentage of total FA composition) for the study area in the southern hemisphere. Contour lines: mean values; black dots: sampling sites

marine habitats (Meyer et al. 2019), beyond just looking at broad marine and terrestrial habitat differences as explored in Colombo et al. (2017) and Gladyshev et al. (2018). Other inter-study comparisons are not so clear, probably due to the complexity of our compiled data set, which included a much broader range of sample types (i.e. different tissues, taxa), and the fact that few meta-analysis FA studies have been performed previously.

4.3. Spatial and temporal patterns and trends

Environment is considered a major factor that influences broad and long-term trends of essential nutrients such as FAs in both terrestrial and marine areas, particularly under the stress of climate change events (Aussant et al. 2018). Environments vary in terms of community composition primary productivity and metabolic rates of resident organisms (Nanton & Castell 1999). At the community level, Meyer et al. (2019) found that temperature was a key driver of 4 FAs (3 PUFA: 22:5n-6, 22:4n-6 and 20:5n-3; and the MUFA 20:1n-9) in Chondrichthyes. Whilst the present study did not directly test the influence of temperature, we did find that samples from polar environments had higher levels of EPA and total MUFA, while DHA and ARA were lower. This finding is in line with other studies showing that polar and temperate marine organisms have higher levels of n-3 PUFA than those from the tropics (Van Ginneken et al. 2011, Colombo et al. 2017). Other studies on Australian fish species have shown higher relative levels of DHA in temperate zones, compared with those sampled in the tropical zones (Nichols et al. 1998, Çelik et al. 2005, Semeniuk et al. 2007). Latitudinal patterns in TLC have been far less studied, though Reinhardt & Van Vleet (1986) showed evidence that marine zooplankton tend to have higher TLC (especially wax ester) at higher latitudes. There is also a general understanding that TLC correlates with primary productivity and thus would be higher in more productive ecosystems such as coastal or upwelling areas (Dunstan et al. 1988, Imbs et al. 2016). Our study showed that the TLC variability of many marine consumers examined was significantly greater in the tropics compared to temperate and polar systems, although the mean TLC was highest for the polar climate species (Fig. 2f).

An increasing number of studies have reported temporal trends in the lipids and FA of marine consumers. This includes reports of seasonal differences in the FA compositions of populations of marine consumers (Pethybridge et al. 2013, Hellessey et al. 2020) that were not detected in this study. Short-term, interannual trends in TLC and individual FAs of marine consumers have also been reported (Groß et al. 2020), with some studies linking trends to changes in primary productivity (e.g. in cephalopods; Pethybridge et al. 2015) or composition of primary producers (Marcus et al. 2016). Few studies have tested long-term (decadal) variability of TLC or FA distribution, although there is increasing evidence that the availability of essential n-3 LC-PUFA is declining as a result of global warming and the associated changes in phytoplankton species composition (Hixson et al. 2015). Furthermore, studies on albacore tuna samples showed that increasing ocean temperatures are impacting the distribution and availability of n-3 LC-PUFA along the coasts of east Australia (Pethybridge et al. 2015) and east Africa (Dhurmeea et al. 2020).

In the present study, we reported an increase in TLC, particularly in storage tissue types, between 2000 to 2004 and then again in 2017, which could indicate an increase in primary productivity in some waters around Australia. While there was high variability in the FAs examined, our work did show some evidence that over time both EPA and ARA have gone through periods of decline, while DHA has increased, which may be due to a possible shift in plankton composition within Australian waters. However, interpretation of these temporal findings is challenged by a number of confounding factors. For example, these shifts could simply reflect changes in the type and number of samples analysed, with a greater number of large vertebrates and liver tissue analysed in recent years, compared to fish or chondrichthyan muscle tissue.

4.4. Challenges and future directions

Given the broad (macroscale) scope of this study, it was difficult to disentangle specific trends, patterns, and effects observed due to several caveats, some of which can be addressed with future research. Firstly, it is essential to acknowledge that meta-analyses of the effects of broadly grouped attributes (tissue, taxa, habitat and environment) reflect records collected in this case over a long temporal window (from 1989 to 2019) and may have been impacted by the weighting of a few dominant species or regional studies with a higher number of records. The inclusion of species that undergo large migrations or movements, such as certain fishes, chondrichthyes and marine mammals, could have greatly influenced any of the observed habitat or environmental effects. While efforts were made to consider finer details, it was beyond the scope of this study to look at other species-level or higher-resolved taxa groups. Future research should also explore taxa, habitat and environmental effects on records of the same tissue type, such as muscle or liver.

It is important to acknowledge that this study only assessed TLC (%WW) and relative FA composition (%TFA) data, and not absolute or concentration data for FA that would allow for more quantitative analysis. Percentage TFA data are typically used in most ecological studies as they are often the only unit reported. Percentage TFA data also best allow for the assessment of trophic linkages through multivariate analysis (Parrish et al. 2015). The primary advantage of presenting FA data as %TFA is that it provides information on trophodynamic relationships. However, without quantitative data, it is difficult to more precisely quantify the amount of essential fatty acids in the organisms or even in marine ecosystems. Another impediment of this meta-analysis study was the lack of an ability to assess the influence of finer body size/length at the taxa or community level, despite body size being a major driver of ecosystem dynamics (Andersen et al. 2016). While the study used trophic position, which is also driven by body size (Dalponti et al. 2018), to gain insights into fish and chondrichthyes, such information is rarely available or easily accessible for invertebrates.

Environmental data (such as satellite-derived products or biogeochemical model outputs for sea surface temperature and chl *a* concentrations) were not obtained or incorporated in this study, as many regional records lacked sufficient precision in geographic coordinates (latitude and longitude) and/or dates (day-month-year) of sample collection. Analysis of such environmental data in combination with TLC and FA data would enable a more comprehensive understanding of how climate change will impact the availability and transport of FAs in marine ecosystems. Future studies should consider the influence of temperature on specific taxa or habitat groups, in order to obtain a better understanding of the complex interactive influence of temperature change and ocean acidification (Ericson et al. 2019). This work could be assisted by including data on other biochemical tracers such as stable carbon and nitro-

gen isotopes or trace elements, to better understand marine ecosystem dynamics.

Many of the caveats described here can be used to implement community best practices with which to guide future research that seeks to undertake lipid and FA analysis of marine samples. For example, all studies should pay particular attention to acquiring and organising metadata on important attributes such as sampling dates, geographical coordinates, total body-size measurements, and quantitative lipid and FA measurements. This would ensure the extended value of their data sets for use in meta-analysis and comparative studies, particularly those seeking to examine any spatial or temporal changes in marine FAs due to climate change or other human impacts.

5. CONCLUSIONS

This study applied a novel meta-analysis approach to gain insights into the main factors that drive biological and spatial-temporal trends of the relative composition of FAs (as %TFA) and the total lipid content (%WW) of marine organisms sampled from waters in the Southern Indian and Pacific Oceans in the southern hemisphere. Taxonomic group, trophic guild, collection period and habitat type were found to be key drivers influencing lipid content and FA composition. Across all taxa groups and climate zones, there is some evidence to suggest that relative levels of EPA have decreased, and DHA increased over the 30 yr period, whilst more variable interannual trends occurred for TLC and ARA. Understanding the spatial and temporal distribution and availability of essential nutrients and energy, including the abundance of the health-benefiting n-3 LC-PUFA is critical for gaining an understanding of marine ecosystem functions and services, which is also important to improve human health and food security. This approach of analysing regional FA data sets will we hope encourage further work by other international laboratories to assess FA patterns and trends across biomes, habitats and taxa. In the future, these data sets can be used to understand the potential effects of temperature change on the regional marine ecosystem and help formulate appropriate strategies to address the impending changes. Further research with the inclusion of data from primary producers, together with the potential expanded use of quantitative FA data, can be used to enhance the investigation of trophic relationships and the health of the wider marine ecosystem.

Data accessibility. Data used for this analysis is available in the published data paper (Nichols et al. 2023) and via an online data portal (https://data.csiro.au/collection/csiro:54636).

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