Lipid storage patterns in marine copepods: environmental, ecological and intrinsic drivers

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ABSTRACT

Seasonality of food supply is a major driver of physiological and ecological adaptations of marine zooplankton. High latitude marine copepods accumulate lipids for maintenance and reproductive maturation during the food-depleted winter period. The relationship between latitude and lipid storage in copepods is well established, but it is influenced by many factors, such as trophic position, sex and depth distribution. In this study, the influence of latitude and collection depth, trophic level, sex and the presence or absence of dormancy on the relative amount and composition of lipids stored was assessed by analysing published data. Our analyses confirmed higher lipid contents (expressed as % dry weight) in high latitude species, and in deep-dwelling tropical copepods compared to shallow-living ones. Contrary to our original hypothesis, carnivorous and herbivorous copepods had similar lipid levels. Copepod species that undergo dormancy had higher levels of wax ester, and were more common at polar and temperate latitudes. Lastly, adult male and female copepods did not significantly differ in the amount of lipids they store, suggesting that the portion of male reproductive investment which may depend on lipid stores has been underestimated. Taken together, these results both confirm some previously reported trends, and refute others.

INTRODUCTION

Copepods are among the most abundant animals on Earth, with some estimates in the order of trillions globally (Humes, 1994). Their ecological importance is due to their trophic position, where they provide a link between their microplanktonic prey species and higher consumers. Copepods make up a major fraction of the diet of fish larvae (Helle, 1994; Turner, 2004; Buckley and Durbin, 2006; Llopiz, 2013; Robert *et al.*, 2014) and planktivorous fish (Dommasnes *et al.*, 2004). In this sense, their role is analogous to that of planktonic protozoans, which link bacterioplankton to metazoan micro- and mesoplankton through "trophic repackaging" (Gifford, 1991). Other copepod predators include chaetognaths (Oresland, 1987), jellyfish (Graham and Kroutil, 2001), baleen whales (Pendleton *et al.*, 2009; Baumgartner *et al.*, 2013) and seabirds (Springer and Roseneau, 1985). Indeed, copepod abundance is a good predictor of the endangered North Atlantic right whale's distribution (Pendleton *et al.*, 2009; Baumgartner *et al.*, 2013). Copepods also contribute to the biological carbon pump, by both active and passive processes, namely vertical migration and faecal pellet production, respectively (reviewed in Turner, 2015). Copepods' input to the biological pump is realised by the utilisation of storage lipids at depth, during periods of diapause (Jónasdóttir *et al.*, 2015). Jónasdóttir *et al*. (2015) quantified the contribution of lipid-replete, diapausing *Calanus finmarchicus* CV copepodids to carbon export in the North Atlantic ("lipid pump"), showing that it is of a similar magnitude to passive sinking processes. This contribution is primarily dependent on copepod stocks at depth, respiration rate and mortality (Jónasdóttir *et al.*, 2015). Therefore, knowledge of the annual lipid accumulation patterns, life cycle and physiology (in particular, metabolic rate at depth) of seasonally migrating copepods is important for assessing their contribution to the biological pump through active carbon transport. In turn, this could be estimated by integrating information on the intrinsic and extrinsic drivers of lipid storage patterns in marine copepod species other than *C. finmarchicus*.

Seasonality of food supply is a major factor affecting biological processes in polar marine species (Clarke, 1988; Arntz *et al.*, 1994; Peck *et al.*, 2006; Peck, 2018). It is considered a major ecological driver of lipid accumulation in high-latitude herbivorous copepods (Conover and Huntley, 1991; Lee *et al.*, 2006). Furthermore, it has been proposed as the main factor limiting growth in polar waters, not just in copepods

(Clarke, 1988; Peck, 2018). Seasonality of predation risk has also been proposed as an underappreciated factor potentially shaping high-latitude copepod life cycles (Kaartvedt, 2000; Varpe, 2012), however its influence on lipid storage has not been investigated. At high latitudes, phytoplankton blooms provide a relatively short window of opportunity for foraging, during which early developmental stages of copepods typically grow at fast rates (Clarke and Peck, 1991; Søreide *et al.*, 2016). At the onset of autumn/winter, late copepodid stages of herbivorous species typically migrate to the deep layers, where they undergo post-embryonic dormancy (or diapause) until the following spring (Lee *et al.*, 2006). Dormancy is characterised by a termination of feeding activity and a marked decrease in metabolic and growth rates (Baumgartner and Tarrant, 2017). There can be substantial deviation from this generalised life cycle, with some species reproducing multiple times a year during the warmer months (multigeneration life cycle), others only reproducing once per life cycle (annual life cycle) and others needing two or more years to complete their life cycle (multiyear cycle, characteristic of some polar herbivorous species), following Conover (1988)'s categorisation. Species with a broad geographical distribution also display considerable intraspecific variation in their life cycles and lipid accumulation patterns. For instance, the life cycle duration of the arctic and subarctic copepod *Calanus hyperboreus* lasts between one and four years, depending on the location (Hirche, 1997 and references therein).

Lipids are used up over the winter period for maintenance and reproductive maturation (Hirche, 1996; Evanson *et al.*, 2000), and copepods start migrating from shallow depths only when they have stored sufficient lipid reserves (the lipid accumulation window hypothesis: Schmid *et al*. (2018)). Mobilised storage lipids also fuel the activity of lecithotrophic early larval stages (nauplii) (Lee *et al.*, 2006). A distinction should be made between species whose life history is characterised by capital breeding on one end of the continuum, where reproduction is fuelled by stored "capital" (Stephens *et al.*, 2009), such as energetic reserves in the form of lipids, and income breeding on the other end, where reproductive costs are met by day-to-day foraging during the reproductive season (Jönsson, 1997; Stephens *et al.*, 2009). Mathematical modelling evidence predicts that for capital breeders, the "sufficiency" of lipid reserves is dependent on the trade-off between predation risk during the foraging season and the benefit of continued feeding for reproductive maturation and/or maintenance during dormancy, while income breeders would store just enough lipids for maintenance (Varpe and Ejsmond, 2018). For omnivorous and carnivorous species, the adaptive significance of lipid storage is less clear, as their food supplies are expected to be less seasonally variable (Clarke, 1988). Nonetheless, some omnivorous and carnivorous copepods have been shown to store large amounts of lipids (Auel and Hagen, 2005), despite not undergoing dormancy and actively feeding throughout winter. For some opportunistic omnivores, such as *Metridia longa*, the phytoplankton bloom still represents the period of maximal prey quality and quantity (Båmstedt and Ervik, 1984). Thus, they are believed to store lipid, albeit to a lesser extent than their herbivorous counterparts, to cope with suboptimal foraging conditions during the winter (Båmstedt and Ervik, 1984). It has been hypothesised that seasonality should contribute less to the life cycle of omnivorous and carnivorous species (Clarke, 1988). However, annual variation in the availability of herbivorous copepods in surface waters may in turn impose a resource limitation for carnivorous species preying on them. This is the case for the planktivorous Atlantic herring *Clupea harengus*, which rapidly increases in body mass (Varpe *et al.*, 2005) and relative lipid content (Stoddard, 1967; McGurk *et al.*, 1980) after a short intensive feeding period in the spring and summer months, when its main prey *C. finmarchicus* is in surface waters.

The two main storage lipid classes in marine copepods are wax ester (WE) and triacylglycerol (TAG). Wax esters are long-chain esters (C_{28}-C_{42}) of diet-derived fatty acids and *de novo* synthesised fatty alcohols (Sargent, 1978), while triacylglycerols are triesters of glycerol and three fatty acid chains. Because dietary fatty acids are generally unmodified, they provide a chemical signature of the different prey taxa consumed by copepods (Graeve *et al.*, 1994; Kattner and Hagen, 1995). Wax esters are the main long-term storage lipids of deep sea and polar marine copepods, while triacylglycerols make up a lesser proportion of the total storage lipids and fuel short-term metabolic needs (Lee and Barnes, 1975; Lee *et al.*, 2006). The Antarctic calanoid *C. propinquus* represents an exception to this, as it stores mainly high-energy triacylglycerols, containing *de novo* elongated fatty acids (Hagen *et al.*, 1993; Kattner *et al.*, 1994). The adaptive significance of wax ester synthesis and storage in most copepod species, as opposed to triacylglycerols, is unclear. According to one hypothesis, wax esters could be synthesised more quickly than triacylglycerols (Bauermeister and Sargent, 1979), however there is no evidence supporting this. Triacylglycerols, on the other hand, are utilised preferentially during short-term starvation, however it is not clear whether this is because they can be catabolised more quickly, as it has been suggested (Lee *et al.*, 2006). Because they are less dense than TAGs (Bauermeister and Sargent, 1979), WEs have been suggested to be important for buoyancy regulation, however several studies have provided evidence against this hypothesis (see Discussion).

The hypothesised key role of seasonality of food supply in shaping polar organisms' life cycles and growth dynamics (Clarke, 1988) allows the following predictions to be made, concerning lipid accumulation in marine copepods.

P1. Total lipid and wax ester contents will be higher with increasing latitude (Lee *et al.*, 1971; Clarke and Peck, 1991).

P2. Upwelling systems at lower latitudes are also highly seasonal (García-Reyes and Largier, 2012; Vidal *et al.*, 2017; Walter *et al.*, 2018; Pinochet *et al.*, 2019), and several copepod species inhabiting them undergo ontogenetic vertical migration and/or dormancy in winter (Peterson, 1998). These species store lipids to an extent comparable to that of their high-latitude counterparts (Verheye *et al.*, 1992; Lee *et al.*, 2006). For this reason, we predict that copepods sampled from areas characterised by upwelling will have a higher lipid and wax ester content than copepods sampled at similar latitudes, but from areas not affected by upwelling.

P3. Lipid and wax ester contents will increase with depth of occurrence, particularly in tropical species (Lee and Hirota, 1973). This is driven not only by seasonality of food supply (i.e. seasonal migrators to the deep sea), but also by the general food limitation of deep sea habitats (Harding, 1974; Smith *et al.*, 2008), which would make lipid storage beneficial for deep-sea copepods (Lee *et al.*, 1971). Although metabolic rate decreases with depth in several taxa (Childress, 1975; Seibel and Drazen, 2007), this does not seem to be the case for copepods (Thuesen and Miller, 1998). Within-species, however, dormant stages typically have a reduced metabolic rate compared to non-dormant ones (Baumgartner and Tarrant, 2017), allowing a slow utilisation of the stored lipids.

P4. Lipid content will be highest in herbivorous species and lowest in omnivorous and carnivorous species, as food supplies for herbivorous species are predominantly restricted to the short summer productive season at high latitudes (Clarke, 1988; Clarke and Peck, 1991) or during upwelling events at lower latitudes (Verheye *et al.*, 1992).

P5. A) In species which undergo dormancy, lipid content will be higher than in non-dormant species, due to the adaptive significance of lipid depots to many polar and temperate species for maintenance during dormancy and reproduction during or after dormancy (Hagen and Auel, 2001). Moreover, wax ester content will also be higher in species undergoing dormancy, given that many of these species are found in high latitude environments and store large amounts of wax esters (Lee *et al.*, 1971). B) Dormancy will be most prevalent at higher latitudes because of the progressively stronger environmental seasonality.

P6. Lipid content may be the same in adult females and males, due to the underappreciated magnitude of spermatophore production costs (Bjærke *et al.*, 2016). Previous laboratory experiments showed that in some species spermatophore production is dependent on food availability (Bjærke *et al.*, 2016), which would suggest a limited dependence on stored lipids. However this is not the case for other species (Burris and Dam, 2015). Studies comparing energetic investment into gametes of male and female copepods are lacking, however male gametogenic investment is known to be equal to or higher than females' in some other marine invertebrates (Tyler *et al.*, 2003; Grange *et al.*, 2004).

Zooplankton lipid dynamics literature is characterised by a multitude of standalone reports, focussed on single or selected few species (see Supplementary Table 1), with some notable exceptions (e.g. Lee, Hirota and Barnett, 1971; Lee and Hirota, 1973). Despite this, some authors have comprehensively reviewed zooplankton lipid accumulation drivers and features (e.g. Hagen and Auel, 2001; Lee, Hagen and Kattner, 2006). The present review aims to expand their work by quantitatively analysing published lipid content data for marine copepods, including almost 100 species. We specifically aim to assess whether lipid content data support the aforementioned predictions, and to explore how various environmental, ecological and intrinsic drivers may shape lipid storage and accumulation strategies in marine copepods.

MATERIALS AND METHODS

Data selection

On July, 31st 2018, a literature search in Web of Science (All Databases) was performed, with the following queries: “copepod* AND (lipid storage OR storage lipid*)” and “zooplankton* AND (lipid storage OR storage lipid*)” (i.e. copepod/zooplankton lipid storage/storage lipids). The results were screened for relevant primary sources, and other references were retrieved from the literature cited in the primary articles.

Three copepod lipid content measures were compiled from the published literature: total lipid (TL) as % dry weight, triglyceride/triacylglycerol (TAG) and wax ester (WE), both expressed as % TL. Additionally, absolute TL content (expressed as µg/individual) was also retrieved from the sources reporting it, however it was not used in the analysis, as it would be expected to change with body size. Where necessary, data were extracted from plots using WebPlotDigitizer 4.1 (Rohatgi, 2018). Only studies where lipids were extracted by chemical methods (i.e. chloroform/dichloromethane:methanol extraction and chromatography-based lipid class analysis) were included in the analysis, therefore excluding lipid sac area/volume-based estimations of lipid content. A list of lipid isolation and lipid class analysis methods used in the selected primary sources is available in Supplementary Table 6. Furthermore, sources which did not report the developmental stage of the sampled copepods were excluded from the dataset.

The following data, when available, were also recorded: collection period, location, depth and sex of the sampled copepods. Species included were further classified into different “feeding guilds” (herbivorous, omnivorous or carnivorous), based on published accounts of their feeding behaviour (from gut content analyses, mouth-part morphology-based assessments, feeding experiments, isotope and marker fatty acids/alcohols analyses). Similarly, information on seasonal (post-embryonic) dormancy (i.e. presence or absence of dormancy in the life cycle) was compiled. For the purpose of this review, dormancy was defined as a period spent at depth below the photic zone without feeding.

Data analysis

For the comparisons among latitudinal zones (P1, see Introduction), feeding guilds (P4), between species undergoing dormancy and those which do not (P5), and between sexes (P6), lipid content measurements of adult females were averaged across studies for each species, without first averaging multiple measurements obtained from the same study (Supplementary Table 2). For species where data were derived from a single source, multiple measurements were averaged for that source where applicable. For the comparison between copepods sampled from upwelling and non-upwelling areas (P2), lipid content measurements of adult females were averaged for each species, but the distinction between upwelling and non-upwelling areas was maintained. Thus, for some species two average values were present, one for samples collected from upwelling areas, one for samples collected from non-upwelling areas (Supplementary Table 3). Similarly, for the comparison among depth classes (P3), lipid content measurements of adult females were averaged for each species, but the distinction between depth classes was maintained. Thus, some species presented more than one average value, e.g. one for samples collected from epipelagic depths and another for samples collected from mesopelagic depths (Supplementary Table 4; see below for definitions of each depth class). Data were not partitioned based on the collection period (i.e. season), so average values include all available data for any one species, regardless of the time sampling. In all instances, the average measure was either the mean or the median TL/TAG/WE content, depending on whether the distribution of the data was normal or not normal, respectively. Data distribution was assessed by inspection of normal Q-Q plots in R (R Core Team, 2018).

The following broad latitudinal categorisations were made: Polar (66.5-90° N or S), Temperate (23.5-66.5° N or S) and Tropical (23.5° N – 23.5° S). Collection depth data in published articles were often reported as ranges. For the purpose of this analysis, depths were therefore categorised as either epipelagic (0-200 m), mesopelagic (201-1000 m) or bathypelagic (1000-4000 m).

Because TAG and WE contents were expected to be negatively correlated, a Spearman's correlation test was performed on the subset of species where data were available for both measures. Adult female lipid content (TL, TAG and WE) was compared among latitudinal classes, feeding guilds and between species that undergo dormancy and those that do not. Lipid content (TL, TAG and WE) of adult female copepods from tropical latitudes was also compared between upwelling vs non-upwelling areas, and among depth classes. The datasets were restricted to adult females for consistency, mainly because data for adult males were relatively scarce in the literature. Moreover, lipid content was compared between sexes, restricting the analysis to adult stages of species where data for both sexes were available. Lastly, lipid content measures (TL, TAG and WE) of copepodid V (CV) stages were compared among latitudinal zones, feeding guilds and between species that undergo dormancy and those that do not. One-way ANOVAs or two-sample t tests were performed if the assumptions of normal distribution and homoscedasticity were met, whereas Kruskal-Wallis or Wilcoxon signed-rank/rank sum tests were performed when they were not. Such assumptions were assessed by Shapiro and Levene's tests respectively, and in some instances the data were transformed ($\log_e$ or square root) to achieve normal distribution and/or homoscedasticity. Posthoc tests (Tukey's test or Dunn's test with Benjamini-Hochberg correction) were performed where applicable, following ANOVA and Kruskal-Wallis tests respectively. The relationship between dormancy and latitude (P5 B) was investigated by performing a two-way Chi-square test, scoring each species as either dormant or not, and assigning it to its respective latitudinal zone. A summary of the analyses performed is presented in Table 1.

All analyses were performed in R, version 3.5.0 (R Core Team, 2018).

RESULTS

A dataset of TL, TAG and WE content measures of 99 species of marine copepods (Supplementary Table 1) was collated from published literature. The data was obtained through database searches yielding a total of 433 sources, of which 40 were selected according to the criteria outlined in the Materials and methods section (Supplementary Table 1). Adult female WE and TAG contents were inversely correlated (Table 1), therefore only the analyses on TL and WE contents are reported. Whilst WE and TAG contents were not correlated in CV stages (Table 1), the analyses were also limited to TL and WE contents for consistency and ease of comparison. TAG content data is available in Supplementary Tables 1-4.

Copepod lipid content changes with latitude, but not between upwelling and non-upwelling areas

Average lipid content values for each species were compared among latitudinal classes representative of where they were collected. Significant differences in total lipid content of adult females were identified among latitudinal zones (Table 1). In particular, polar copepods had significantly higher TL content than temperate and polar ones (Figure 1A). On the other hand, there were no significant differences in WE contents of adult females among latitudinal zones (Table 1), however polar copepods also appeared to have the highest WE content (Figure 1B). TL and WE contents of CVs were not significantly different among latitudinal zones (Table 1; Supplementary Figure 1).

Lipid content measures were also compared between copepods collected from upwelling vs non-upwelling areas at tropical latitudes. There was no significant difference in TL or WE contents of adult female tropical copepods collected from upwelling areas compared to those collected from non-upwelling areas (Table 1; Supplementary Figure 2).

Tropical deep-sea copepods have higher lipid content than shallow-living ones

The influence of collection depth on tropical copepods' lipid content was investigated. TL content of adult females was significantly different among depth classes (Table 1), with copepods sampled from the bathypelagic zone having a significantly higher TL content than those sampled from the epipelagic zone (Figure 2A). This was not the case for WEs (Table 1; Figure 2B). The analysis was repeated including only tropical copepods sampled from non-upwelling areas, to minimise the effect of dormancy and ontogenetic vertical migration on copepod lipid storage in upwelling areas. In this subset, there were no significant differences in TL or WE contents among depth classes (Table 1; Supplementary Figure 3).

Carnivorous copepods store more lipids than omnivorous ones

In order to determine whether diet may affect the amount of stored lipid in copepods, lipid content measures were compared among herbivorous, omnivorous and carnivorous species. TL and WE contents were significantly higher in carnivorous species compared to omnivorous ones (adult female subset, Table 1; Figure 3). The same did not hold true for CVs (Table 1; Supplementary Figure 4).

Copepods undergoing dormancy store more wax esters than those which do not

Lastly, the effect of dormancy on copepod lipid storage strategies was assessed, by comparing species which undergo dormancy with those that do not. Moreover, the relationship between the occurrence of dormancy and latitude was investigated. While there was no significant difference in TL content between species exhibiting and not exhibiting dormancy (Table 1; Figure 4A), the difference was clearly significant for WE content (Table 1; Figure 4B), which was higher in the former group (Figure 4B). On the other hand, CV copepod TL and WE contents did not vary significantly between species exhibiting or not exhibiting dormancy (Table 1; Supplementary Figure 5). There was a significant relationship between the occurrence of dormancy and latitudinal zone (Table 1). Species exhibiting dormancy were almost entirely restricted to polar and temperate latitudes, with only one tropical species out of 61 undergoing dormancy in its life cycle (Figure 4C).

Female and male copepods do not differ in the amount of stored lipids

Lipid content measures were also compared between sexes, in species where data were available for both sexes. Adult male and female copepods did not differ significantly in their TL or WE contents (Table 1; Supplementary Figure 6).

DISCUSSION

The present study aimed to quantitatively assess the influence of environmental, life cycle and biological factors on lipid accumulation patterns in marine copepods. In particular, six predictions (P1-6, see Introduction), were tested by analysing copepod lipid content data retrieved from the primary literature.

Our analyses demonstrated that TL content in copepods increased with latitude (Figure 1) in an expected fashion (P1), however tropical species sampled from upwelling areas did not store more TL or WE than those from non-upwelling areas, as hypothesised (P2). The results confirmed our initial prediction (P3) that tropical deeper-living copepods would have higher lipid content than shallow-living species (Figure 2A). This was not the case, however, for WEs (Figure 2B). Contrary to expectations (P4), carnivores had higher TL and WE contents than omnivorous species, and their TL and WE levels were similar to herbivores' (Figure 3B). Species exhibiting dormancy had higher WE contents than those that did not (Figure 4B), as expected (P5). Lastly, male and female copepods did not store significantly different amounts of lipids (Supplementary Figure 6), as was expected from P6. These points are dealt with in more detail below. CV stages broadly showed the same lipid accumulation trends as adult females (Supplementary Figures 1, 4 and 5), however none of the factors analysed (latitude, depth and life cycles including dormancy) had a significant effect on TL or WE contents (Table 1). Given the considerably smaller sample sizes of the CV analyses (Table 1), this is likely a result of lower statistical power compared to the analyses restricted to adult females.

Lipid storage data compiled in the present study were uneven across latitudinal regions: north temperate and tropical copepods comprised 72 out of 94 species where data were available (adult females subset, see Supplementary Table 1). Of these, 44 were tropical and 28 were north temperate, which aligns with the trend of relatively high diversity of copepods in tropical regions, that gradually decreases in north temperate and north polar regions, reported by Rombouts *et al*. (2009). South temperate copepods however, despite being relatively diverse (Rombouts *et al.*, 2009), only comprised 6 out of 94 species in the present dataset (Supplementary Table 2). This suggests that a sampling bias may be, at least partially, responsible for the latitudinal imbalance of lipid content data available in the literature, and highlights a paucity of data and research in the southern hemisphere.

Influence of latitude and upwelling on lipid content and composition

Polar and temperate copepod species have previously been reported to have higher TL and WE contents than tropical species (Lee *et al.*, 1971; Lee and Hirota, 1973). Hence, TL and WE contents were expected to increase with latitude (P1, see Introduction). The present analysis broadly confirmed this prediction for adult females (Figure 1), but not for CVs (Supplementary Figure 1). Copepods store lipids primarily for overwintering and/or reproduction in seasonal environments (Hagen and Schnack-Schiel, 1996; Varpe *et al.*, 2009; Maps *et al.*, 2014). Indeed, seasonality shapes many aspects of polar and temperate species' life cycles (Arntz *et al.*, 1994; Peck *et al.*, 2006; Peck, 2018), as exemplified by the high incidence and adaptive value of capital breeding at these latitudes (Varpe *et al.*, 2009). Wax esters followed the same trend (Figure 1B), which is not surprising, considering that most species primarily use WEs for storage (Supplementary Table 2). In fact, of the species where data were available for TAG and WE contents, only 27 out of 67 primarily stored TAGs, of which 16 were tropical and with low TL levels (mostly < 20 % of dry mass). Nevenzel (1970) proposed two hypotheses to explain the function of wax ester accumulation: to aid buoyancy and as an energy reserve. The role of WEs in buoyancy regulation has been the subject of ongoing debate in the scientific literature since then. Evidence from theoretical models and empirical data suggests that accumulation of WEs alone cannot be responsible for prolonged periods of neutral buoyancy at depth (Campbell, 2003). Instead, Campbell (2003) proposed that ionic buoyancy regulation may be employed by vertically migrating copepods, as is the case for many other pelagic marine invertebrates (Barnes *et al.*, 2001). Although high haemolymph ammonium concentrations have been recorded in Antarctic copepod species, these do not appear to change with depth (Sartoris *et al.*, 2010) or season (Schründer *et al.*, 2013), suggesting that other factors may be at play. More recently, copepods have been hypothesised to control their buoyancy by modulating WE fatty alcohol saturation level, which would in turn affect the depth at which neutral buoyancy is achieved (Pond, 2012). If this was the case, there would be a clear advantage in storing WEs over TAGs, perhaps explaining the high incidence of WE as the main storage lipid in copepods (Pond, 2012), and the prevalence of WEs at high latitudes (Figure 1B). However, WEs are also major constituents of many non-diapausing tropical copepods' storage lipids (e.g. *Paraeuchaeta* spp., *Gaussia princeps*, *Megacalanus princeps*, *Gaetanus pileatus*, etc., see

Supplementary Table 2), raising questions on whether the adaptive significance of this lipid class in these species is in fact related to buoyancy.

In contrast to WEs, triacylglycerols (TAGs) are believed to provide for short-term energy needs in most copepods, and they are preferentially utilised during starvation (Lee and Barnes, 1975; Mauchline, 1998; Lee *et al.*, 2006). However, there are exceptions, i.e. species which use TAGs as storage lipids (e.g. *Calanus propinquus*, *Euchirella rostromagna*, *Paralabidocera antarctica*, etc., see Supplementary Table 2). In particular, *Calanus simillimus*, *Eucalanus bungii* and *E. californicus* not only primarily store TAGs, but also undergo dormancy at depth (Supplementary Table 2). Considering the relatively minor contribution of WEs to their TL content, it is likely that these species do not rely on WEs for buoyancy regulation (see above). The molecular and physiological mechanisms underpinning preferential TAG utilisation during short-term starvation are largely unknown. The evolutionarily conserved 3-hydroxyacyl-CoA dehydrogenase enzyme is central to fatty acid β-oxidation, and its activity is often used as a general biomarker for lipid catabolism (Hassett, 2006; Freese *et al.*, 2016). However, it is unclear how lipid catabolic pathways are regulated in short-term TAG breakdown as opposed to long-term WE utilisation.

Tropical copepods in upwelling regions such as the Benguela and Humboldt upwelling systems are characterised by high relative lipid content, comparable to high latitude species (Lee *et al.*, 2006). Despite this, our analysis showed that copepods sampled in upwelling areas at tropical latitudes did not significantly differ in the amount of TL or WE they accumulated compared to ones sampled in non-upwelling areas (Supplementary Figure 2). It should be noted, however, that this analysis was based on a limited number of sources (Table 1), which presented lipid content data for only a small number of geographical regions, and thus these data should be interpreted with care. The timing of dormancy and stage succession dynamics of tropical copepods in upwelling areas are not well understood, and the life-cycle information available has been described as “rudimentary” (Peterson, 1998). Lipid content data from a wider range of locations and with a higher temporal resolution will be needed in order to definitively rule out a difference in lipid accumulation strategies between copepods found in upwelling *vs* non-upwelling areas at tropical latitudes.

Influence of depth on lipid storage in tropical copepods

The intraspecific differences in lipid content between depth zones are well established in ontogenetic migrants (Lee *et al.*, 2006), reflecting a need to store lipids for overwintering at depth. Interspecific differences in lipid content between shallow- and deep-dwelling species have been observed in copepods (Lee *et al.*, 1971) and zooplankton in general (Clarke and Peck, 1991), especially from tropical and subtropical latitudes. These observations are supported by our analysis, as there was a trend of increasing TL and WE contents from the epipelagic to the bathypelagic zone (Figure 2), and a significantly higher TL content in copepods collected from bathypelagic vs epipelagic depths (Figure 2A). There was a large variability in WE content (Figure 2B), with values ranging from 0.1 to 91 % of TL (Supplementary Figure 4). In an attempt to reduce this variability, an additional analysis restricted to tropical species collected from non-upwelling areas was performed (Table 1). The differences seen between depth zones were less clear in this subset (Supplementary Figure 3), likely due to the much smaller sample size. It should be noted that, in the vast majority of studies compiled, copepods were collected by vertical hauls to the surface, thus making depth comparisons difficult. Future studies should use higher resolution stratified sampling to facilitate wider scale interspecific comparisons of lipid storage patterns and other traits that may vary with depth of occurrence in copepods.

The effect of diet on lipid content and composition

Herbivorous copepods from high latitudes rely on a highly seasonal food supply, especially in polar zones, while omnivorous species often stay active during the winter (Graeve *et al.*, 1994; Hagen and Auel, 2001). Likewise, carnivorous species tend to feed all year round (Øresland and Ward, 1993). Winter feeding in omnivorous and carnivorous species not only translates to lower lipid reserves than in herbivorous species (Clarke and Peck, 1991; Graeve *et al.*, 1994; Mauchline, 1998), but also to slower lipid turnover in conditions of high prey abundance (Boissonnot *et al.*, 2016). Whether the slower incorporation of diet-derived lipids into storage depots in omnivorous/carnivorous copepods is caused by fundamentally different physiological mechanisms of lipid utilisation between omnivorous/carnivorous species and herbivorous ones is not known. Because omnivorous and carnivorous copepods continue feeding during the winter, it was predicted that they would have lower lipid content than herbivorous species (P4, see Introduction). Surprisingly, in the present analysis TL and WE contents were not significantly different between herbivorous and carnivorous copepods (Figure 3). On the other hand, carnivorous copepods had significantly higher TL and WE contents than omnivorous species (Figure 3). Lipid-rich carnivorous species are well known, and lipid storage patterns are particularly well documented in *Paraeuchaeta* spp. (Auel and Hagen, 2005). Despite the fact that *Paraeuchaeta* spp. seem to continue feeding throughout the winter (Øresland and Ward, 1993), TL levels change seasonally and peak in the summer/autumn in epi-mesopelagic species (Auel and Hagen, 2005) such as *P. antarctica* (Figure 5). However, this seasonal trend is considerably less pronounced than in some herbivorous species (e.g. *Calanoides acutus*, see Figure 5). The seasonal trend in TL levels may be driven by sub-optimal feeding conditions during the winter, however the stark ontogenetic pattern of TL accumulation suggests that a large fraction of the stored lipids is invested into eggs and early developmental stages, which do not start feeding until CIII-IV (Auel and Hagen, 2005). If other carnivorous copepods were characterised by a comparably high reproductive investment, this could explain their relatively high TL and WE contents (Figure 3). High lipid content in carnivorous copepods may also be explained by the potential limitation imposed by the seasonal fluctuations in prey abundance, e.g. herbivorous copepod “standing crop” (Clarke, 1988). Nonetheless, the adaptive significance of a high lipid content in carnivorous copepods remains unresolved. Most seasonal studies have focussed on diapausing herbivorous species, while carnivorous copepods have been assumed to stay active during the winter and to feed throughout. Future investigations should assess the seasonal patterns of lipid storage, feeding patterns and depth distribution of carnivorous copepods, with a particular focus on reproductive investment and energy use during winter.

A higher lipid content in carnivorous zooplankton would have potential implications for bioaccumulation (and possibly biomagnification) of lipophilic pollutants. Indeed, bioaccumulation potential increases with lipid content (LeBlanc, 1995), which in turn, as shown here, increases with trophic level in copepods. Moreover, bioaccumulation has been shown to be greater for pollutants taken up via feeding than passively through the surrounding water (Magnusson and Tiselius, 2010), although this was not the case for less recalcitrant pollutants such as polycyclic aromatic hydrocarbons (Arias *et al.*, 2016). This suggests that the trophic link between herbivorous and carnivorous copepods would potentially be a prime route for the bioaccumulation of lipophilic compounds. Indeed, field evidence supports this hypothesis, as organic pollutant concentrations in carnivorous zooplankton and ice-associated fauna are higher than in herbivorous species in the Arctic (Borgå *et al.*, 2002; Hallanger *et al.*, 2011). However, laboratory experiments taking into account lipid content and composition of zooplankton are needed to identify the exact mechanisms of bioaccumulation between different trophic levels.

The relationship between lipid storage and the occurrence of dormancy in copepods from different latitudinal zones

It was predicted that species undergoing dormancy in their life cycles would have a higher lipid content than ones not exhibiting dormancy (P5 A, see Introduction). Our data did not have sufficient temporal resolution to allow differentiation between seasons, but time of sampling is expected to influence lipid content measures, e.g. in the pre- *vs* post-dormancy periods. Nonetheless, the present analysis supported our prediction, especially when considering WE content (Figure 4B). Only one tropical species undergoing dormancy was identified: *Rhincalanus nasutus* in the Red Sea (Schnack-Schiel *et al.*, 2008). Because of vertical mixing effects this species has a highly seasonal food supply (Farstey, 2001). All other species exhibiting dormancy were from polar or temperate latitudes (Figure 4C), and species from these latitudes were significantly more likely to exhibit dormancy in their life cycle (Table 1). In support of our result, a recent modelling study determined food availability (i.e. phytoplankton bloom dynamics) and temperature to be two major factors influencing seasonal vertical migration timing in high latitude environments (Bandara *et al.*, 2018). In the North Atlantic, phytoplankton blooms initiate later and are shorter with increasing latitude (Friedland *et al.*, 2016). However, a recent analysis of satellite-obtained chlorophyll concentration data collected between 1997 and 2007 reported that the relationship between bloom duration and latitude was not linear (Sapiano *et al.*, 2012). On the contrary, bloom duration was demonstrated to vary zonally rather than latitudinally on a global scale (Sapiano *et al.*, 2012). This could potentially explain the higher number of temperate species undergoing dormancy compared to polar ones (Figure 4C). The relationship between dormancy duration, lipid storage and latitude (or phytoplankton bloom duration) remains to be determined, especially when comparing temperate and polar species (Figure 4C). Modelling approaches (e.g. Maps *et al.*, 2014; Bandara *et al.*, 2018), coupled with high quality field and satellite data, hold great promise.

Lipid storage and reproductive cycles

There is a wealth of studies highlighting the relationship between lipid storage and gonad maturation in female copepods (e.g. Hirche and Kattner, 1993; Hagen and Schnack-Schiel, 1996; Hirche, 1996), which have traditionally been thought to invest more energy than males in sexual maturation (Gatten *et al.*, 1980). Male copepods generally have a higher mortality rate than females (Kiørboe, 2006), serving the "brief function" of reproduction (Conover, 1988). In some species, this is due to males having a naturally shorter lifespan than females. For instance, virgin *Oithona davisae* males live almost half as long as virgin females (Ceballos and Kiørboe, 2011). Many studies investigating changes in gonad mass upon spawning in other marine invertebrates show little or no difference between males and females (Grange *et al.*, 2004, 2007) and some studies reported higher reproductive investment by males than females, for example in the Antarctic scallop *Adamussium colbecki* (Tyler *et al.*, 2003). Male reproductive investment in copepods is not well-characterised (Titelman *et al.*, 2007), and recent studies suggest that it could be higher than previously thought (Bjærke *et al.*, 2016). In *Calanus glacialis* and *C. finmarchicus*, males develop earlier than females and before the phytoplankton bloom, suggesting that their gonad maturation is entirely reliant on lipid stores (Tande and Hopkins, 1981; Kosobokova, 1999). Kosobokova (1999) argued that the production of spermatozoa may be relatively more expensive in energy terms than ova on a unit mass basis, as they contain more energetically-costly proteinaceous material. There were no significant differences in lipid content between adults of the two sexes in the present analysis (Supplementary Figure 6), indicating that overall energy cycles are very likely similar, and that male reproductive investment, if dependent on lipid stores, could bear a similar energetic cost to females. However, making general conclusions should only be done with great care, considering that lipid content information for adult males was only available for 22 out of 99 species (Supplementary Table 2).

Summary and outlook

The present analysis provides support for the well-established trend for higher lipid content with increasing latitude in copepods, confirming Clarke and Peck (1991)'s observed trend for zooplankton in general. This is likely due to the larger effect of seasonality, as lipid-rich diapausing species tend to inhabit polar and temperate basins (Figure 4C). However, the effect of seasonality is modulated by the life cycle and feeding habits of copepods, as exemplified by the seasonal lipid dynamics of four sympatric Antarctic copepods (Figure 5). Carnivorous copepods, unexpectedly, had higher lipid content than omnivorous species, and some species were influenced by seasonality, though to a lesser extent than herbivorous species (see Figure 5). Lipid content was not statistically different between male and female copepods, suggesting that the portion of male reproductive investment which may depend on lipid stores has been underestimated (Bjærke *et al.*, 2016). The results presented here highlight a need for further research in several areas. Firstly, annual field surveys should be conducted to elucidate carnivorous species' life cycles: their high lipid content cannot be assumed to be constant throughout the year (see Figure 5). In general, field surveys should include depth-stratified sampling, in order to pinpoint the role of depth in shaping copepods' lipid storage patterns. Secondly, male reproductive investment and lipid storage patterns, which have also been neglected in the literature, need to be quantified by field and experimental studies. Thirdly, exact sample sizes (n) for each sample used to determine lipid content or composition should be clearly reported instead of ranges, as this will allow more rigorous analyses of available data. Lastly, our dataset revealed a striking sampling imbalance against south temperate species, despite copepods being very diverse in this region (Rombouts *et al.*, 2009). Thus, there is a compelling need for more field surveys south of the Equator.

SUPPLEMENTARY MATERIAL

The following supplementary material is available at *ICESJMS* online: ICES_Supplementary_Tables (Excel file). Supplementary Table 1 contains the raw lipid content data, as extracted from the literature. Supplementary Table 2 contains the average lipid content data used for the latitudinal, feeding guild, dormancy and sex analyses (P1, P4, P5, P6, see Introduction). Supplementary Table 3 contains average lipid content data used for the comparison between copepods sampled from upwelling vs non-upwelling areas (P2). Supplementary Table 4 contains average lipid content data used for the depth analysis (P3). Supplementary Table 5 contains high temporal resolution lipid content data of four sympatric species (see Figure 5). Supplementary Table 6 contains a breakdown of the lipid extraction methods used.

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AUTHOR CONTRIBUTIONS

A. C. collated and analysed the data. L. S. P. conceived the study and obtained the funding. A. C. and L. S. P. interpreted the results and co-wrote the original draft.

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FIGURE LEGENDS

Figure 1. Total lipid content (A) and wax ester content (B) of adult female copepods across latitudinal zones. The boxplots show the medians and interquartile ranges, while the open circle represents an outlier. Significant differences between latitudinal zones ($p < 0.05$) are denoted with an asterisk, and sample sizes are reported below latitudinal zone names. Data were derived from primary literature listed in Supplementary Table 2.

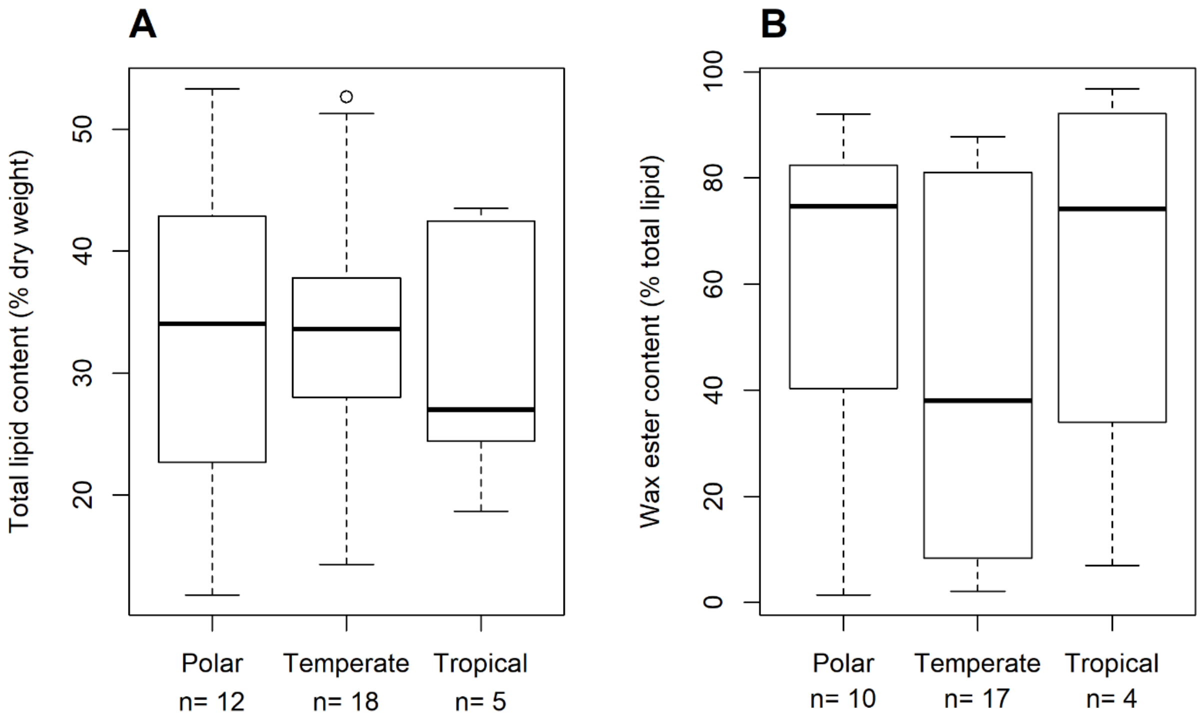
Figure 2. Total lipid content (A) and wax ester content (B) of tropical copepods sampled from epipelagic, mesopelagic and bathypelagic depths. The boxplots show the medians and interquartile ranges, while the open circles represent outliers. Significant differences between feeding guilds ($p < 0.05$) are denoted with an asterisk, and sample sizes are reported below latitudinal zone names. Abbreviations: E = epipelagic, M = mesopelagic, B = bathypelagic. Data were derived from primary literature listed in Supplementary Table 4.

Figure 3. Total lipid content (A) and wax ester content (B) of herbivorous, omnivorous and carnivorous adult female copepods. The boxplots show the medians and interquartile ranges, while the open circles represent outliers. Significant differences between feeding guilds are denoted with one ($p < 0.05$) or two ($p < 0.01$) asterisk(s), and sample sizes are reported below feeding guild names. Data were derived from primary literature listed in Supplementary Table 2.

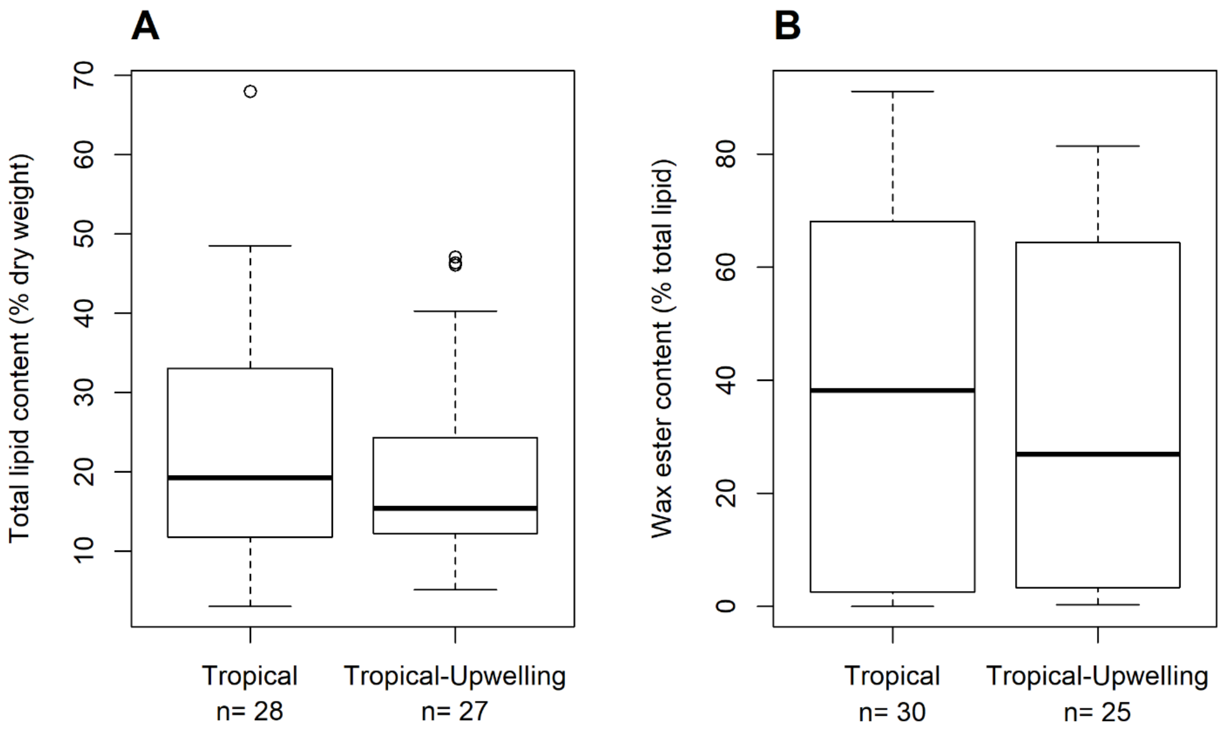
Figure 4. Total lipid content (A) and wax ester content (B) of adult female copepods undergoing dormancy in their life cycle *vs* non-dormant ones. **Number of copepod species undergoing and not undergoing dormancy across latitudinal zones (C)**. The boxplots show the medians and interquartile ranges, while the open circle represents an outlier. Significant differences ($p < 0.05$) between non-dormant and dormant species are denoted with an asterisk, and sample sizes are reported below the group names. Data were derived from primary literature listed in Supplementary Table 2.

Figure 5. Seasonal changes in total lipid content of four representative copepod species belonging to different feeding guilds, sampled from the Weddell Sea. Data were derived from primary literature listed in Supplementary Table 5. Jan-Feb months correspond to the summer period, while Apr-May, Jul-Aug and

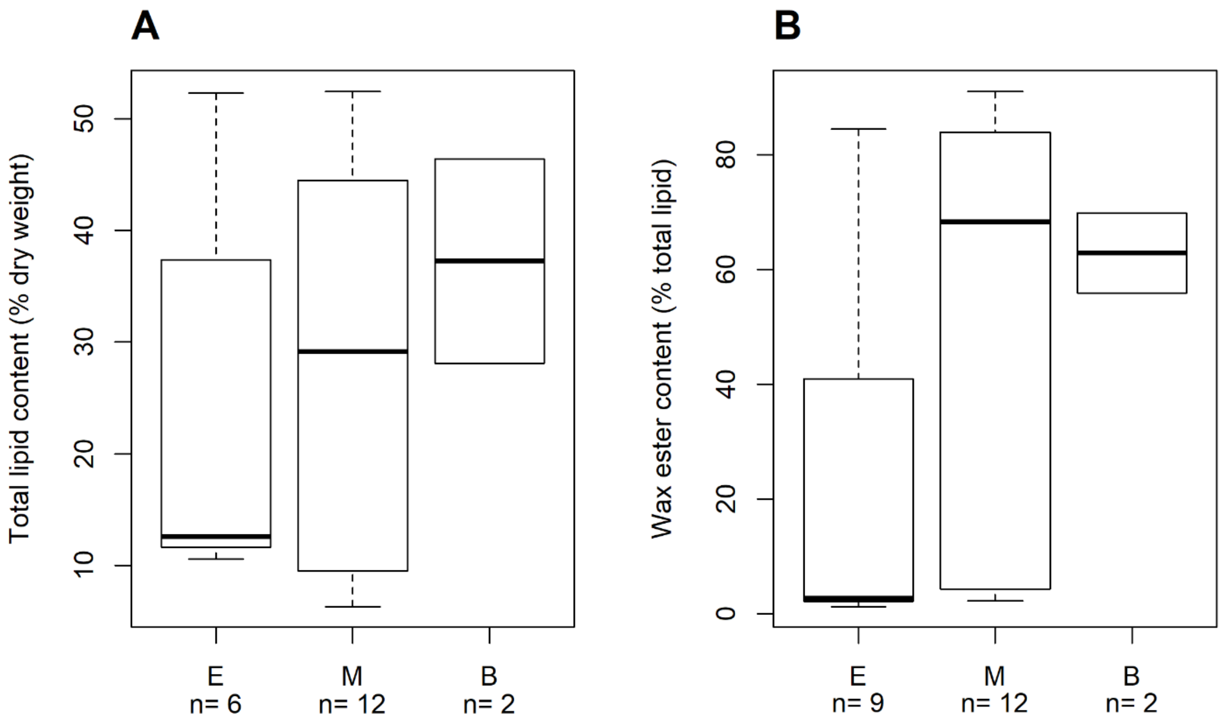
Oct-Nov correspond to the early, mid- and late winter periods. The boxplots show the medians and interquartile ranges, while the open circles represent outliers. A line connecting the medians was added to highlight seasonal changes. For *Calanoides acutus*, the dormancy period is denoted by the dashed line.



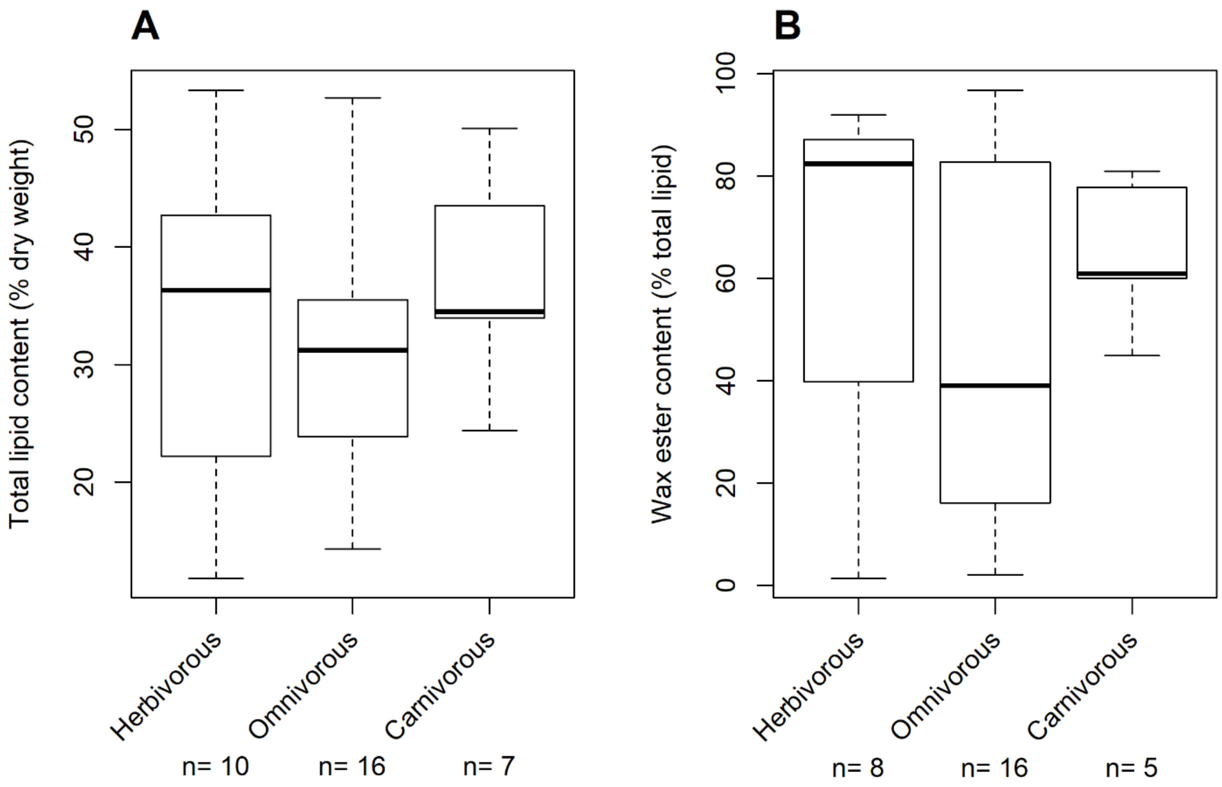
Supplementary Figure 1. Total lipid content (A) and wax ester content (B) of copepodid V (CV) copepods across latitudinal zones. The boxplots show the medians and interquartile ranges, while the open circle represents an outlier. Sample sizes are reported below latitudinal zone names. Data were derived from primary literature listed in Supplementary Table 2.



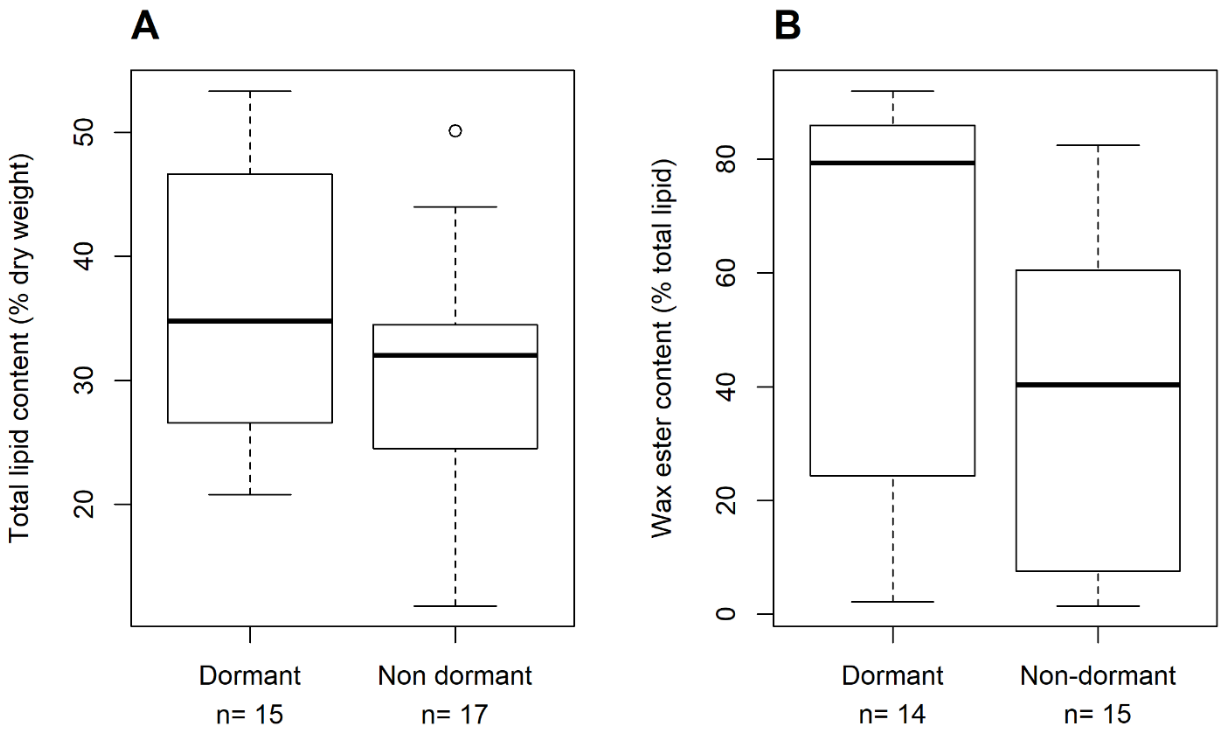
Supplementary Figure 2. Total lipid content (A) and wax ester content (B) of tropical copepods (adult females only) sampled from upwelling ("Tropical-Upwelling") and non-upwelling ("Tropical") areas. The boxplots show the medians and interquartile ranges, while the open circles represent outliers. Sample sizes are reported below the plots. Data were derived from primary literature listed in Supplementary Table 3.



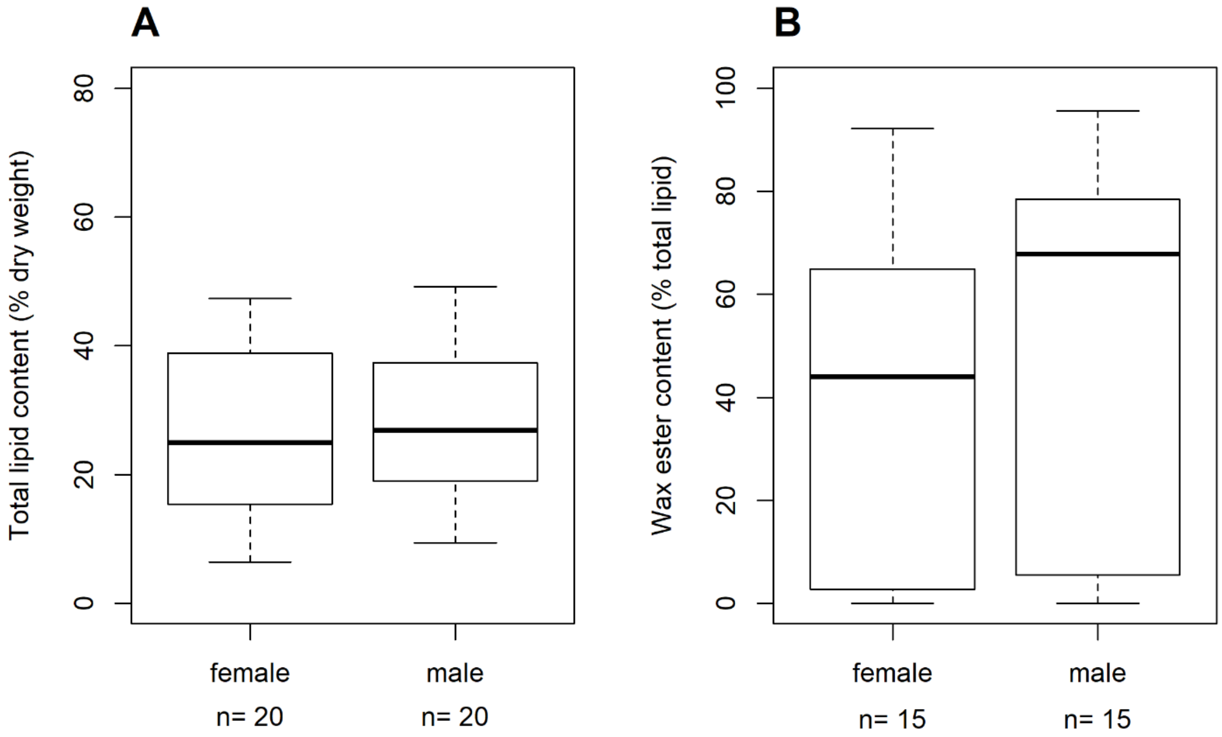
Supplementary Figure 3. Total lipid content (A) and wax ester content (B) of tropical copepods (adult females collected from non-upwelling areas only) sampled from different depth classes. The boxplots show the medians and interquartile ranges. Sample sizes are reported below the plots. Abbreviations: E = epipelagic, M = mesopelagic, B = bathypelagic. Data were derived from primary literature listed in Supplementary Table 4.



Supplementary Figure 4. Total lipid content (A) and wax ester content (B) of herbivorous, omnivorous and carnivorous CV stage copepods. The boxplots show the medians and interquartile ranges. Sample sizes are reported below feeding guild names. Data were derived from primary literature listed in Supplementary Table 2.



Supplementary Figure 5. Total lipid content (A) and wax ester content (B) of CV stage copepods undergoing dormancy in their life cycle vs non-dormant ones. The boxplots show the medians and interquartile ranges, while the open circle represents an outlier. Sample sizes are reported below the plots. Data were derived from primary literature listed in Supplementary Table 2.



Supplementary Figure 6. Total lipid content (A) and wax ester content (B) of adult female and male copepod species where data was available for both sexes. The boxplots show the medians and interquartile ranges. Sample sizes are reported below the plots. Data were derived from primary literature listed in Supplementary Table 2.

Table 1 Summary of the analyses performed. Sample sizes (n) refer to the number of species in each factor level, except for the upwelling vs non-upwelling and depth comparisons, where some species had more than one average lipid content measure (e.g. one for samples collected from epipelagic depths and one for samples collected from mesopelagic depths), see Methods section.

Analysis	**Subset**	**Number of data sources**	**Lipid content measure**	**Sample sizes**	**Effect**
WE and TAG correlation	Adult females, species where both WE and TAG data were available	25	TAG and WE (% TL)	n = 66	Spearman's correlation $r_s = -0.508$, **$p = 1.314 \times 10^{-5}$**
	CV, species where both WE and TAG data were available	17	TAG and WE (% TL)	n = 21	Spearman's correlation $r_s = -0.407$, p = 0.067
Latitude	Adult females	39	TL (% DW)	Polar: n = 16 Temperate: n = 32 Tropical: n = 41	Kruskal-Wallis test $X^2 = 8.661$, df = 2, **p = 0.013**
		32	WE (% TL)	Polar: n = 13 Temperate: n = 29 Tropical: n = 40	Kruskal-Wallis test $X^2 = 5.531$, df = 2, p = 0.063
	CV	31	TL (% DW)	Polar: n = 12 Temperate: n = 18 Tropical: n = 5	ANOVA $F_{2,32} = 0.108$, p = 0.898
		25	WE (% TL)	Polar: n = 10 Temperate: n = 17 Tropical: n = 4	Kruskal-Wallis test $X^2 = 1.514$, df = 2, p = 0.469
Upwelling vs non-upwelling	Tropical species, adult females	6	TL (% DW)	Upwelling: n = 27 Non-upwelling: n = 28	ANOVA $F_{1,53} = 0.368$, p = 0.547
		7	WE (% TL)	Upwelling: n = 30 Non-upwelling: n = 25	Kruskal-Wallis test $X^2 = 0.064$, df = 1, p = 0.800
Depth	Tropical species, adult females	4	TL (% DW)	Epipelagic: n = 17 Mesopelagic: n = 28 Bathypelagic: n = 4	ANOVA $F_{2,46} = 3.666$, **p = 0.033**
		5	WE (% TL)	Epipelagic: n = 18 Mesopelagic: n = 27 Bathypelagic: n = 4	Kruskal-Wallis test $X^2 = 4.833$, df = 2, p = 0.089
	Tropical species from non-upwelling areas, adult females	2	TL (% DW)	Epipelagic: n = 6 Mesopelagic: n = 12 Bathypelagic: n = 2	ANOVA $F_{2,17} = 0.583$, p = 0.569
		3	WE (% TL)	Epipelagic: n = 9 Mesopelagic: n = 12 Bathypelagic: n = 2	ANOVA $F_{2,20} = 1.589$, p = 0.229
Feeding guild	Adult females	40	TL (% DW)	Herbivorous: n = 13 Omnivorous: n = 42 Carnivorous: n = 27	ANOVA $F_{2,79} = 4.201$, **p = 0.018**
		33	WE (% TL)	Herbivorous: n = 10 Omnivorous: n = 40	ANOVA

				Carnivorous: n = 24	$F_{2,71} = 4.800$, **p = 0.011**
	CV	32	TL (% DW)	Herbivorous: n = 10 Omnivorous: n = 16 Carnivorous: n = 7	ANOVA $F_{2,30} = 0.660$, p = 0.524
		25	WE (% TL)	Herbivorous: n = 8 Omnivorous: n = 16 Carnivorous: n = 5	ANOVA $F_{2,26} = 0.973$, p = 0.391
Sex	Adults, species with data for both sexes	23	TL (% DW)	Females: n = 20 Males: n = 20	Paired two-sample t-test $t_{19} = -0.849$, p = 0.406
		16	WE (% TL)	Females: n = 15 Males: n = 15	Wilcoxon singed-rank test V = 25, p = 0.090
Dormancy	Adult females	40	TL (% DW)	Dormancy present: n = 14 Dormancy absent: n = 49	Two sample t-test $t_{23.39} = 2.057$, p = 0.051
		32	WE (% TL)	Dormancy present: n = 14 Dormancy absent: n = 42	Wilcoxon rank sum test W = 421.5, **p = 0.016**
	CV	30	TL (% DW)	Dormancy present: n = 15 Dormancy absent: n = 17	Two sample t-test $T_{27.68} = 1.271$, p = 0.214
		23	WE (% TL)	Dormancy present: n = 14 Dormancy absent: n = 15	Wilcoxon rank sum test W = 147, p = 0.070
Relationship between dormancy and latitude	Species with information about both dormancy and collection zone	41	N/A	Dormancy present: n = 14 Dormancy absent: n = 47 Polar: n = 15 Temperate: n = 24 Tropical: n = 22	Chi-squared test $X^2_2 = 6.592$, **p = 0.037**