



Research



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Author for correspondence:

Sigrun Jonasdottir

e-mail: sjo@aqua.dtu.dk

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Diatom–lipid–copepod nexus under threat by global change

Sigrun Jonasdottir¹, Richard Broughton² and André Visser¹

¹Department of Ocean Science and Technology, Technical University of Denmark, National Institute of Aquatic Resources, Kongens Lyngby, Denmark

²Institute of Aquaculture, University of Stirling, Stirling, UK

SJ, 0000-0003-4985-0447

The central role of lipids in the ecology of high-latitude and temperate seas is under threat by global change. This hinges on the tight ecological links between diatoms and copepods of the genus *Calanus* and similar (e.g. *Neocalanus*, *Calanoides*) that produce and accumulate energy-rich lipids. Strongly coupled through seasonal water-column stability, nutrient supply, spring-bloom succession, and overwintering life strategies, this nexus is foundational to the highly productive food webs of these regions. We experimentally tested how a change in phytoplankton type from diatoms to flagellates, along with 2°C warming, affects lipid accumulation of the subarctic copepod *Calanus finmarchicus*. We report that the ability of *C. finmarchicus* to accumulate lipids is seriously impaired by a changing diet, being threefold higher on diatoms than flagellate-based diets, whereas within diet types, up to a sevenfold reduction in lipids is associated with a 2°C temperature rise. This, together with higher specific respiration rates, smaller size, and reduced diatom productivity, suggests the ability of *Calanus* to overwinter may be compromised, threatening their contribution to regional productivity and to sequestered carbon via the lipid pump. Similar lipid-mediated couplings are prevalent throughout seasonal environments, casting uncertainty on their future provision of ecosystem services.

1. Introduction

The dominance of diatoms in seasonal productivity cycles appears to be waning [1–4]. This is part of a broader climate-induced shift in phytoplankton communities as large areas of sub-polar and temperate seas become increasingly stratified, reducing the annual replenishment of nutrients to the sunlit surface ocean. Although a complex mix of many factors (temperature, light, nutrients, and traits), the general trend can be likened to a poleward expansion of sub-tropical-like conditions with a commensurate shift in plankton taxa and production cycles [3,5]. Notably, productivity will become more dependent on the microbial loop and recycled nutrients, shifting primary producer communities away from diatoms towards smaller phytoplankton cells [2] and will significantly impact food web energy transfer efficiency. Importantly, because diatoms are a rich source of lipids (typically 25% of carbon mass [6]), the availability of lipids to these polar and sub-polar ecosystems will probably be reduced.

Lipid-rich copepods are the foundation of high-latitude marine ecosystems and form a direct link between primary production by diatoms and other phytoplankton to fish, seabirds and marine mammals [7,8]. Members of the genus *Calanus* are particularly conspicuous owing to their large size (2–7 mm), high

abundance and energy content. Their success stems from their life history trait to accumulate lipids (wax esters, WE) constituting typically 60% of their body volume and enter diapause (hibernation) at depth for up to 9 months of the year, avoiding high predation risk at the surface when food availability is limited [9]. This life history trait is commonly adopted by copepods in seasonal environments such as polar and temperate ecosystems, monsoons, and upwelling areas [10] and drives the lipid pump; the active vertical transport and storage of carbon by diapausing copepods through respiration at meso- and bathypelagic depths [11].

The accumulation of lipids is crucial, both as an energy source to fuel respiration during diapause and reproduction upon emergence the following spring, but also to maintain neutral buoyancy while in a torpid state [12]. In the North Atlantic, this is typified by the prominent species *Calanus finmarchicus* that starts lipid accumulation after metamorphosis from nauplii to copepodite and reaches maximum level in copepod stage 5 (C5), after which they descend to diapause. Although the triggers for the initiation, duration, and emergence from diapause are probably a mix of environmental cues and genetic coding, the efficacy of diapause is critically dependent on the amount and type of lipids as well as overwintering temperatures [13–15]. With too little lipid, or high diapause temperatures, the reserves will be depleted before emergence takes place, or the copepods will ascend with reduced reserves for gonad development and reproduction. Furthermore, the faster individuals can build the requisite lipid reserves, the sooner they can descend for safety at depth [14]. Thus, irrespective of what controls diapause timing, impaired lipid accumulation will invariably lead to lowered fitness, through either reduced survivorship or reduced reproductivity, a situation exacerbated by warming overwintering temperatures.

In this work, we investigate the impact of different diets and temperature on lipid accumulation, WE saturation and vital rates of a typical overwintering copepod, *C. finmarchicus*. We did this with the energy budget of overwintering strategies in mind. This is a laboratory study, but with clear implications for natural systems under climate change.

2. Methods

(a) Copepod culturing and experimental setup

C. finmarchicus females were collected in Disko Bay, Greenland, in April, and transported live to Denmark. Females were cultured in a mixture of water from the Labrador Sea and artificial seawater at 33 psu. They were fed a mixture (approx. equal carbon ratio) of healthy growing cryptophyte *Rhodomonas salina* (Rs), diatom *Thalassiosira weissflogii* (Tw; *syn. Conticribra weissflogii*), and dinoflagellate *Heterocapsa triquetra* (Ht) ad libitum. The size of the cells was measured with a Coulter Counter (Beckman Coulter, Multisizer 4), resulting in ESD: 7, 14, and 16 μm for Rs, Tw, and Ht, respectively. The cell carbon values of 98 and 131 pgC cell^{-1} for Rs and Tw, respectively, were attained from [16] measured on exponentially growing cultures, and the value of 319 pgC cell^{-1} for Ht was calculated on the basis of cell volume [17]. The respective experimental temperatures of 5 and 7°C were applied from the start of the female culturing. All copepod culturing and feeding trials were conducted in darkness in a walk-in temperature-controlled room, and gentle aeration was applied at all times.

Eggs were harvested and distributed into 20 l beakers with filtered seawater at the experimental temperature. Approximately 1000 eggs were put in each beaker. When hatched, the nauplii at the first feeding stage N2 were fed the same food mixture as above at a more controlled concentration of 400 $\mu\text{gC l}^{-1}$.

Metamorphosis turned out to be a major bottleneck in copepod development, often resulting in bent antennae or mortality. Following metamorphosis to the C1 stage, the population was divided into three treatment groups. Each treatment began with about 75 healthy, non-damaged C1 individuals, initially split into three 2-l bottles containing about 25 individuals. The treatments consisted of pure diets of the experimental food Rs, Tw and Ht at an excess food concentration of 400 $\mu\text{gC l}^{-1}$. Copepod densities were set based on size-based estimated ingestion rates [18] to ensure that the food concentration would not fall under 250 $\mu\text{gC l}^{-1}$ within 2–3 days. Naupliar (mixed diet) and copepodite (pure diet) cultures were maintained by replacing 80% of the water two to three times a week. This was done by reverse filtration of the culture vessels, followed by replenishment with fresh seawater and food. Mortality was not monitored. After 2 weeks, the volume of the incubation containers was increased to 5 l to accommodate growing copepodites, and copepodite densities were adjusted accordingly. Owing to these adjustments of volume and copepod concentration throughout the experiment, it became difficult to maintain clearly distinct unmixed replicates within treatments.

For all treatments, the experiment was terminated on the same day—during which most of the copepodites had reached copepodite stage 5 (C5), whereas some were still at stage 4 (C4). This took about 20 and 34 days for 7°C and 5°C, respectively. All individuals from the treatments were photographed through a Leica-S9i stereomicroscope, and a group of four to five individuals was sorted into dry tapered glass vials, topped with nitrogen gas and frozen at –80°C for WE analysis.

From the images, the copepod prosome length and oil sac area (OSA) were traced using ImageJ software [19]. The pixel-to-mm ratio was calibrated using the image of the appropriate calibration slide. OSA was converted into WEs using the formula $\text{WE (mg)} = 0.167 \times A^{1.42}$ from [20], where A is the area of the lipid sac in mm^2 .

(b) Wax ester analysis

As the degree of saturation (i.e. number of double bonds) in WEs can affect the physical properties of the lipids and therefore depth of diapause [15,21], we assessed whether the different diets influenced the properties of copepod WEs.

Copepods were weighed and counted into polypropylene tubes using 5–40 mg of sample and extracted in 10 µl of a 0.2 mg ml⁻¹ butylated hydroxytoluene solution in 50:50 water/methanol, followed by 350 µl of 90:10 methanol/water solution. Three glass beads were added to each vial and the sample homogenized using a bead beater at 2000 r.p.m. for 30 s. Following this, 1000 µl of methyl tert-butyl ether (MTBE) was added and the sample vortexed and left at room temperature for 5 min. Phase partition was ensured by adding 250 µl of water, followed by vortexing and centrifugation at 10 000 r.p.m. for 5 min. The upper MTBE phase was then transferred with glass pipettes into clean Eppendorf tubes, and the original samples re-extracted in the same way with 1000 µl of MTBE that was subsequently pooled with the first extract. Samples were dried under a stream of nitrogen and resuspended in 1 ml of 2:1 MTBE/methanol solution. Depending on the amount of sample available, various dilutions ranging from 1 in 5 to 1 in 80 were used to allow for optimum column loading for each sample.

Samples were analysed using supercritical fluid chromatography (SFC-ESI-MS/MS) on an Acquity UPC2 system (Waters, USA) as described previously [22], using a method similar to the neutral lipid separation. Separation conditions were kept the same, with mass spectra acquired over a smaller range, 50–1000 Da, using the data-dependent mode and a ramped collision energy of 28–40 V for the product ion scan.

Unsaturation and carbon number indexes of the copepod WE were calculated, representing the number of double bonds and carbon, respectively.

Unsaturation index (average double bond number):

$$\frac{1}{100} \Sigma (1 \times (\text{monoene}\%) + (2 \times (\text{diene}\%)) + (3 \times (\text{triene}\%)) + (n \times (\text{N}\%))).$$

Average carbon number (WEs):

$$\frac{1}{100} \Sigma (28 \times (\text{C28 WE}\%) + (30 \times (\text{C30 WE}\%)) + (32 \times (\text{C32 WE}\%)) + (n \times (\text{CnWE}\%))).$$

Both indices are unitless.

(c) Calculations

To put the findings into context, we calculate representative estimates of relevant parameters and vital rates for each treatment. These are reported in italics in table 1.

- Maximum carbon-based WE content* is estimated as described in [9,23] and is based on structural carbon mass m scaled to prosome length (p [mm]) as: $m = \alpha p^3$ and WE carbon mass $w_{\max} = \beta p^3$. The coefficients $\alpha = 14 \mu\text{gC}^{1/4} \text{ mm}^{-1}$ and $\beta = 19 \mu\text{gC}^{1/4} \text{ mm}^{-1}$ are defined by a best-fit regression of observed structural carbon and maximum WE carbon content of *C. finmarchicus* versus prosome length p [9]. WE carbon is estimated as 79% of the WE mass [24].
- Respiration rate* [$\mu\text{gC ind}^{-1} \text{ d}^{-1}$] is based on structural mass m of individual copepods following the model of [23] and applied to *C. finmarchicus* in [9]. Following standard metabolic theory, respiration rate is given by

$$r = bm^{3/4} \exp(E(T - T_0) / (kTT_0))$$

[23,25], where $E = (0.6 \pm 0.1) \text{ eV}$ is the activation energy, $k = 8.61733 \times 10^{-5} \text{ eV K}^{-1}$ is the Boltzmann constant, T is the absolute temperature (in K), and T_0 is a reference temperature taken as 273 K. The metabolic constant used here is $b = (1.9 \pm 0.4) \times 10^{-7} \mu\text{gC}^{1/4} \text{ s}^{-1}$, appropriate for overwintering *C. finmarchicus* [25] and slightly lower than $b = (2.3 \pm 0.4) \times 10^{-7} \mu\text{gC}^{1/4} \text{ s}^{-1}$, the metabolic constant for a wide range of species of overwintering copepods [25]. Note that the specific respiration rate $r^* = r/m \mu\text{gC} \mu\text{gC}^{-1} \text{ d}^{-1}$ can be readily estimated from the above.

- Lipid accumulation rate* [$\mu\text{gC ind}^{-1} \text{ d}^{-1}$] is computed by dividing carbon-based lipid content by the length of the experiment.

(d) Statistical analysis

Differences between means were tested using one-way ANOVA (for prosome length, saturation index, and carbon length index) and the Kruskal–Wallis one-way analysis of ranks (for WE content). Pairwise multiple comparisons were conducted using the Dunn or Holm–Sidak methods, respectively.

3. Results and discussion

We tested lipid accumulation rates of *C. finmarchicus* reared from stage C1 to C5 on pure diets of high nutritional quality. Our interest was in quantifying animal size and lipid mass, rather than lipid ratios as is usual in these types of studies. The diets

Table 1. Summary of results for *C. finmarchicus* stages C4 and C5 at 7 and 5°C feeding trials.

temperature 5°C	C4 Rs	C4 Tw	C4 Ht	C5 Rs	C5 Tw	C5 Ht
number of measures length/lipids	24/23	18/17	18	23/20	19/18	31
length of experiment (d)	34	34	34	34	34	34
oil sac area, OSA, mm ²	0.10 ± 0.02	0.26 ± 0.03	0.03 ± 0.01	0.15 ± 0.02	0.41 ± 0.03	0.14 ± 0.02
(a) lipid C max capacity (%)	5	15	2	5	18	5
(b) respiration rate µgC ind ⁻¹ d ⁻¹	0.61	0.68	0.48	0.92	0.95	0.93
diapause respiration at -0.5°C	0.37	0.41	0.29	0.56	0.57	0.56
(c) lipid accumulation µgC ind ⁻¹ d ⁻¹	0.1 ± 0.2	0.6 ± 0.2	0.03 ± 0.03	0.3 ± 0.1	1.1 ± 0.2	0.2 ± 0.1

temperature 7°C	C4 Rs	C4 Tw	C4 Ht	C5 Rs	C5 Tw	C5 Ht
number of measures length/lipids	36	12/11	4	22	67/66	17
length of experiment (d)	20	20	20	20	20	20
oil sac area, OSA, mm ²	0.03 ± 0.01	0.11 ± 0.01	0.00 ± 0.00	0.06 ± 0.01	0.43 ± 0.01	0.07 ± 0.02
(a) lipid C max capacity (%)	2	9	0	3	30	3
(b) respiration rate µgC ind ⁻¹ d ⁻¹	0.38	0.46	0.45	0.71	0.83	0.73
diapause respiration at -0.5°C	0.19	0.23	0.23	0.36	0.42	0.37
(c) lipid accumulation µgC ind ⁻¹ d ⁻¹	0.1 ± 0.1	0.3 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	2.1 ± 0.3	0.2 ± 0.2

Values calculated according to (a) to (d) described in §2.

represented the predicted change from a diatom to dinoflagellate and flagellate-based food web. The trials also tested temperature change of a predicted 2°C from 5 to 7°C, which is within the current thermal tolerance of this species [9]. The results show clearly that diatoms are crucial to the lipid accumulation strategy of polar copepods. Stages C4 and C5 were significantly smaller (by 19 and 14%, respectively) when grown at 7°C compared with 5°C (figure 1a). Copepods feeding on the diatom *Thalassiosira weissflogii* (Tw) had notably larger lipid sacs compared with those feeding on the cryptophyte *Rhodomonas salina* (Rs) and the dinoflagellate *Heterocapsa triquetra* (Ht; figure 2a–c). When translated to WEs, diatom-fed C4s and C5s had 3- to 15-fold higher WE content (figure 1b) and filled up to 30% of their size-based WE carbon capacity compared with a maximum of 5% for those fed on Rs and Ht (figure 1b; table 1).

Temperature did not affect lipid sac size in stage C5, but the lipid sac was significantly smaller at 7°C compared with 5°C for stage C4. When estimating lipid accumulation rates over the experimental period, rates were generally lower at 7°C than at 5°C, with the exception of C5 individuals fed the Tw diet (table 1).

Copepodites C4 are still allocating energy to somatic growth, whereas C5s have largely ceased growth. Thus, for C4s, the different responses at 5°C and 7°C may be explained by increased metabolic costs at higher temperatures, reducing lipid accumulation.

In the case of the contrasting results for C5 copepods feeding on the Tw diet, lipid sac size did not differ significantly between temperature treatments. However, the experimental period was longer at 5°C (34 d) than at 7°C (20 d), resulting in lower estimated accumulation rates at the lower temperature. This pattern may reflect temperature-dependent physiological processes. Q_{10} values for copepod respiration (2–3) are typically lower than those for feeding (1–8) [26], suggesting that relatively higher ingestion rates at 7°C could promote increased lipid accumulation. These results certainly warrant further investigation.

The unsaturation index of copepod WE did not differ significantly among treatments (figure 1c), except in individuals feeding on Ht, which displayed the highest degree of unsaturation. Similarly, the index of carbon chain length of the WE was generally consistent across treatments, although the lowest values were observed in individuals fed the Tw diet. Overall, these findings suggest that the physical properties of the lipids—and consequently buoyancy and diapause depth—are unlikely to vary substantially among the three dietary treatments.

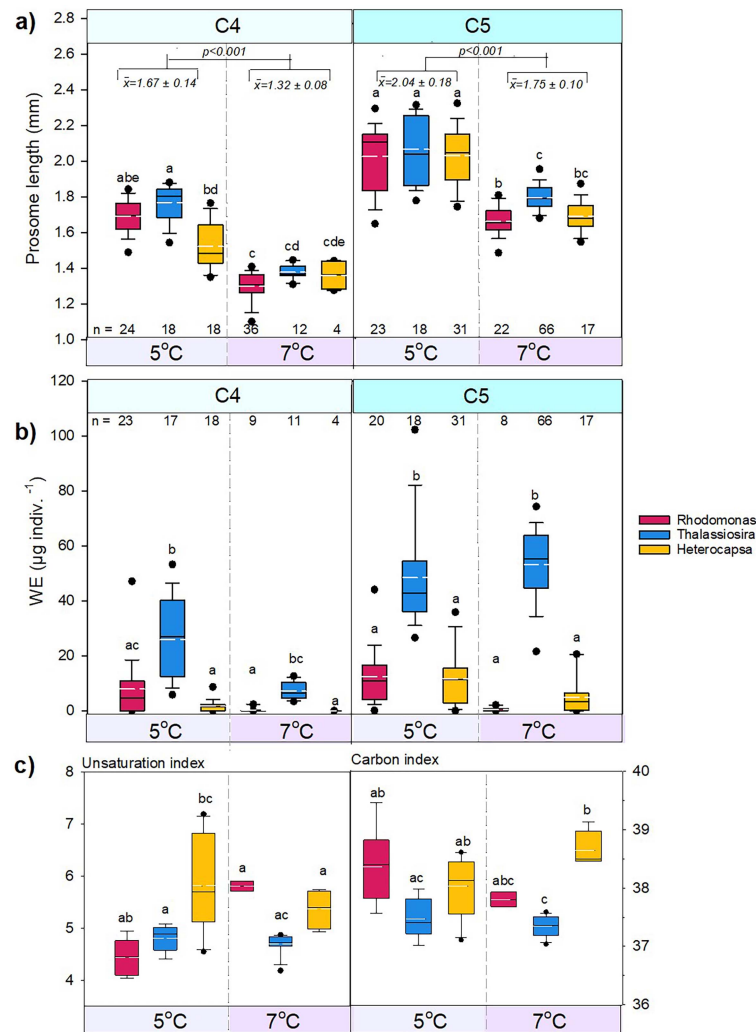


Figure 1. *C. finmarchicus*. Box diagrams of prosome length (mm) (a), WE content ($\mu\text{g individual}^{-1}$) of stage C4 and C5 (b), and WE unsaturation and carbon indexes of combined C4 and C5 (c) after feeding the three different phytoplankton species *Rhodomonas salina* (red), *Thalassiosira weissflogii* (blue), and *Heterocapsa triquetra* (yellow) at 5°C and 7°C. The box, whiskers, and solid dots outline 25/75, 90/10, and 95/5 percentiles. Solid line, median; dotted white line, mean. Lowercase letters indicate no significant difference ($p > 0.05$) between those sharing the same letter within stages (a,b) and temperatures (c). n , number of measures. In (a), average $\pm$ s.d. of the prosome lengths and the p -value of the ANOVA within stages.

Regardless of the physiological reason, the diatom diet results in faster lipid accumulation, allowing earlier descent from the surface to deeper waters [14], reducing population predation pressure and increasing survival. The copepods feeding on flagellate- and dinoflagellate-based diets will, on the other hand, need considerably more time to reach a similar level of lipid reserves (table 1).

These results indicate three compounding effects, each impacting the ability of *C. finmarchicus* to successfully overwinter. First, lipid accumulation depends critically on the presence of diatoms, where lipid accumulation rate and WE fullness (percentage of lipid C capacity) are 3- to 15-fold higher on diatom- than on flagellate-based diets. Second, increasing temperatures both at the surface and (potentially) at depth mean higher metabolic rates with faster usage of lipids. Finally, reduced size of maturing individuals also plays a critical role. Larger individuals can store a greater mass of lipids, yet the specific metabolic requirement for overwintering a given time is a decreasing function of the individual's structural mass. Thus, under the same conditions, larger individuals can overwinter longer and/or produce a greater number of nutritionally supplied eggs upon ascent to the surface the following spring [9]. The compounding effects of reduced lipid availability, smaller size at maturation, and higher metabolic rates may prove a significant hurdle to the life-history strategies that make these copepods such key actors in high-latitude and temperate ecosystems.

Although our immediate focus is on the North Atlantic and Arctic, changing phytoplankton taxonomic composition is a common feature of many high-latitude and temperate ecosystems [3,4]. It is evident that community structures are shifting away from diatoms and copepods towards a greater abundance of flagellates [3]. A unifying feature of these systems is the efficient transfer of lipids from diatoms to large zooplankton (copepods and krill), providing both reserves for overwintering and an efficient trophic

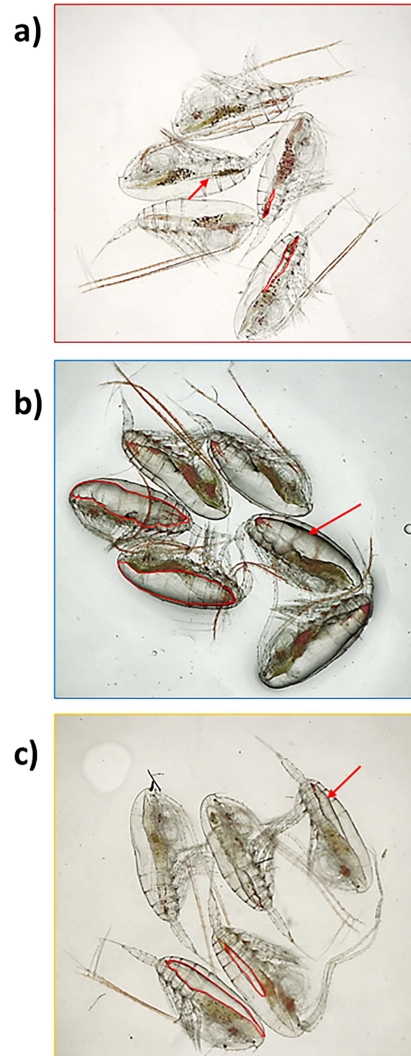


Figure 2. *C. finmarchicus* stage C5 at end of experiment at 7°C, after feeding on *R. salina* (a), *T. weissflogii* (b), and *H. triquetra* (c). The oil sac is the clear structure shown by arrows and outlined in some individuals by red solid lines.

link to higher trophic levels [27]. Reduced ability of these large zooplankton to accumulate lipids poses an existential risk to these taxa, with repercussions for global productivity and carbon sequestration.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The datasets supporting this article are available in Zenodo [28,29].

Supplementary material is available online [30].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Author's contributions. S.J.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, validation, writing—original draft, writing—review and editing; R.B.: formal analysis, funding acquisition, resources, writing—review and editing; A.V.: funding acquisition, methodology, resources, validation, writing—original draft, writing—review and editing.

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Conflict of interest declaration. We declare we have no competing interests.

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