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Energy content of krill and amphipods in the Barents Sea from summer to winter: variation across species and size

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Abstract

Arctic zooplankton develop large energy reserves, as an adaptation to strong seasonality, making them valuable prey items. We quantified the energy content (kJ g^{-1} dry weight) of abundant krill (arcto-boreal, *Thysanoessa inermis* and boreal, *Meganyctiphanes norvegica*) and amphipods (Arctic, *Themisto libellula* and sub-Arctic-boreal, *Themisto abyssorum*) in the Barents Sea in late summer (August) and early winter (December). Variation in energy content was attributed to species-specific traits and body size categories, the latter in part as a proxy for ontogeny. *T. inermis* had the highest energy content, (Aug: 26.8 ± 1.5 (SD) kJ g^{-1}) and remained similar from summer to winter. Energy content increased in *M. norvegica* and decreased in both amphipod species, with the lowest energy content being in *T. abyssorum* (Dec: 17.8 ± 0.8 kJ g^{-1}). The effect of body size varied between species, with energy content increasing with size in *T. inermis* and *T. libellula*, and no change with size in *M. norvegica* and *T. abyssorum*. The reproductive stages of *T. libellula* differed in energy content, being highest in gravid females. Energy content varied with species' dependence on energy storage. Our findings highlight how phylogenetically and morphologically similar prey items cannot necessarily be considered equal from a predator´s perspective. Energetically, the northern *T. inermis* was higher quality compared to the more southern *M. norvegica*, and mostly so during summer. Ecological models and management strategies should consider such variation in prey quality, especially as Arctic borealization is expected to change species composition and the energetic landscape for predators.

Keywords Energy density · Seasonality · Bomb calorimetry · Life history strategies · Lipids · Borealization · Macrozooplankton

Introduction

Energy flux is a key component in an ecosystem's functioning (Barnes et al. 2018). Inherent to this flux, from primary producers to apex predators, is the energy content of an organism (Brown et al. 2004; Van de Putte et al. 2006). Prey quality typically increases with energy content and thereby impacts the foraging behaviour and prey choice in consumers (Lawson et al. 1998; Houston and McNamara 1999; Spitz et al. 2010a). Thus, quantifying the energy content of key species in an ecosystem is an important step in understanding food web dynamics, energy flux and overall ecosystem functioning.

However, an organism does not exist in a constant state, but rather experiences physical, physiological and behavioural changes throughout its lifetime, and through the year. This variability is apparent with changes in body size and developmental stage, where trade-offs in the energy allocated to growth and reproduction occur over an annual cycle and throughout a lifetime (Perrin and Sibly 1993; McNamara and Houston 1996; Stearns 2000). Seasonal environmental variables, such as food availability, shape life history and foraging strategies, which in turn impact selection pressures on energy storage and allocation (Varpe 2017).

Arctic marine ecosystems have strong seasonality, in particular through changing light conditions, sea ice cover and

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primary production (Ji et al. 2013). Arctic zooplankton species have evolved adaptations to this seasonal environment, notably through their use of energy reserves. Many Arctic species develop prominent lipid stores to survive periods of low food availability, as well as use reserves to fuel reproduction ahead of the productive period (i.e. capital breeding), rather than depend on concurrent food intake (i.e. income breeding) (Hagen 1999; Varpe et al. 2009; Daase et al. 2013).

In Arctic and sub-Arctic seas, macrozooplankton such as krill and amphipods are an important dietary link between primary and secondary producers and higher trophic levels, being prey items of fish (Cusa et al. 2019; Eriksen et al. 2021), seabirds (Mehlum and Gabrielsen 1993; Dalpadado 2001) and marine mammals (Falk-Petersen et al. 2004). The Barents Sea is highly productive and one of the most biodiverse marine ecosystems in the Arctic (Sakshaug et al. 1994; Michel et al. 2012; Dalpadado et al. 2020). Both Arctic and Atlantic water influenced, the Barents Sea hosts Arctic and boreal species of macrozooplankton, including krill, such as the arcto-boreal *Thysanoessa inermis* and the boreal *Meganyctiphanes norvegica*, as well as amphipods, such as the Arctic *Themisto libellula* and the sub-Arctic-boreal *Themisto abyssorum*. These species make for interesting comparisons of species-specific traits related to feeding and reproductive strategies, and how these differences may affect energy content. However, there are only a few studies that explore the energetic dynamics of these important prey species, as outlined below.

To our knowledge, only two studies so far report energy content of these krill and amphipod species for the Barents Sea region (Mårtensson et al. 1996; Weslawski et al. 1999). More so, a key seasonal transition in the Arctic is the shift from summer to winter, from the productive to the relatively unproductive period. However, most of the existing studies for these species take place almost exclusively in the summer months (Percy and Fife 1981; Kulka and Corey 1982; Wolowicz and Szaniawska 1986; Weslawski et al. 1999, 2000; Walkusz et al. 2012) excluding energetic changes occurring in the lead up and during winter. Indeed, we are not aware of winter energy content data for these macrozooplankton species from the Barents Sea region. Borealization, with sub-Arctic species already seen to be moving northwards into warming Arctic waters (Fossheim et al. 2015), is also expected to alter current species composition in the Barents Sea and may impact the quality of prey available for predators (CAFF 2017; Griffith et al. 2019). It is important to understand the energetic dynamics of key prey species, such as krill and amphipods, to predict the effects such changes will have on the functioning of a future Arctic system.

The aim of this study is to quantify the energy content of abundant macrozooplankton species, making comparison between Arctic and boreal species, namely the krill *T. inermis* and *M. norvegica*, and the amphipods *T. libellula* and *T. abyssorum*, in the late summer and early winter in the Barents Sea. We investigate how energetic changes from the productive to unproductive period are related to the feeding and life history strategies and annual routines of these species. We categorise individuals into size classes, to investigate the effect of different developmental stages on changes in energy allocation. We also compare the early winter energy content of male and female *T. libellula*. Additionally, we summarise energy content estimates from the literature for these species and review our results in the context of these works.

Methods

Study site, species, and sample collection

The target macrozooplankton species were sampled at six stations along a transect from 76° N to 82° N in the Barents Sea during late summer (August 4–27, 2019, SQ3, Nansen Legacy project) and at nine stations in early winter (November 28–December 17, 2019, SQ4, Nansen Legacy project) on-board RV Kronprins Haakon (Fig. 1).

At the sampling stations in open water, a Methot Isaac Kidd (MIK) net (13 m length, 2 m diameter, 1.5-mm mesh, with rear 1.5 m 500-μm mesh) was towed as an oblique haul, or a macrozooplankton trawl was used. In ice covered water, the MIK net was towed vertically. At each station, the entire water column was sampled, from 20 m above the bottom depth to the surface. At the northernmost station, where bottom depth exceeded 3000 m, nets were taken from 1000 m and 500 m to the surface, due to limitations of wire time.

Macrozooplankton were sorted to species level in cold seawater on ice, to keep individuals alive and prevent degradation. Using millimetre paper, individuals from each species were measured to the nearest millimetre and sorted into size classes: 0–10 mm, 11–20 mm, 21–30 mm and 31–40 mm. Amphipods, *T. libellula* and *T. abyssorum*, were measured from the front of the head to the tip of the longest uropod (Dunbar 1957). Krill, *T. inermis* and *M. norvegica,* were measured from the anterior edge of the eye to the tip of the telson, excluding the setae (Mauchline and Fisher 1969). The size classes represent a rough estimation of life stage. Within each size class, individuals that were collected at the same sampling station, or sometimes at two consecutive stations, were pooled together to achieve a bulk sample with a minimum wet weight of 1 g. This minimum weight is required to have enough biological material for energetic analyses. In cases where bulk samples were less than 1 g, then multiple samples would be pooled together to have enough material for analysis. If bulk samples were large enough, multiple subsamples were taken and used to make replicate pellets for bomb calorimetry. The number of individuals per sample varied depending on species and life

Fig. 1 Map showing wider
European Arctic (inlay) and
the Barents Sea (main) with
summer (August) and winter
(December) transects and sam-
pling stations indicated for each
cruise. The ice edge, as defined
by the limit between "very open
drift ice" and open water, is
indicated by the white dashed
lines for August and December.
Ice edge is based on satellite
data from the 12th day of each
month. Map provided by Bernt
Bye, Norwegian Polar Institute
(2021)
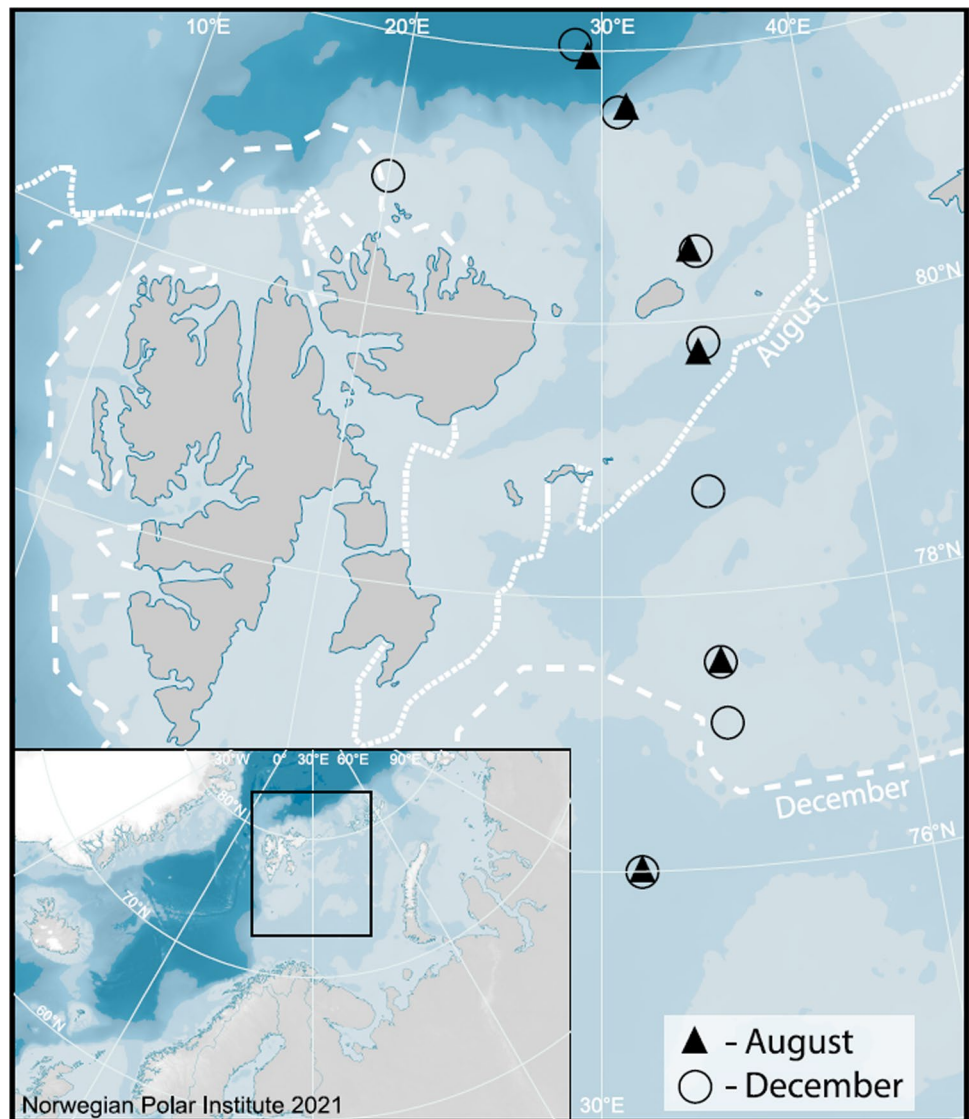
stage. The samples were weighed and stored in aluminium
foil at -20℃ until analysis. The number of samples for each
species, season and size class combination varied, due to
sampling effort and the abundance of krill and amphipods.

During the winter cruise, sexually mature individuals of
T. libellula were observed and sampled. Males were identi-
fied by the presence of long antennae and gravid females
were identified by the presence of eggs in the brood pouch.
Therefore, winter samples of this species were classified as
undetermined sex, male or gravid female.

Details on the distribution within the Barents Sea, average
adult body size, feeding strategy, and reproductive strategy
and breeding season were summarised for the four species
of macrozooplankton in this study (Table 1). Capital breed-
ing is when energy reserves are used to fuel reproduction, as
opposed to income breeding which is when reproduction is
dependent on concurrent energy intake (Varpe et al. 2009).

Capital and income breeding are extremes on a gradient, and
many species combine elements of the two, which can be
referred to as mixed breeding (Varpe and Ejsmond 2018).
References in Table 1 do not explicitly use capital-income
terminology, and the capital-income terms we apply in
Table 1 are approximations of where they lie on this repro-
ductive spectrum.

Energy content

Energy content was measured using a Parr® 6725 Semi-
micro Oxygen Bomb Calorimeter. Frozen samples were
freeze-dried for a minimum of 24 h, after which the dry
weight of each sample was determined. Dried samples
were homogenised using a pestle and mortar. Using the
Parr® 2812 Pellet Press, subsamples were taken from the
bulk homogenised sample and pressed into pellets roughly

Table 1 Summarized information regarding the focus species of this study on energy content in macrozooplankton of the Barents Sea

	Krill		Amphipods	
	Thysanoessa inermis	*Meganyctiphanes norvegica*	*Themisto libellula*	*Themisto abyssorum*
Distribution within the Barents Sea	Southern and Western Barents Sea (Arcto-boreal)[a]	Atlantic waters and Southern Barents Sea (boreal)[a]	Predominately Arctic waters, Central and Northern Barents Sea (Arctic)[g]	Predominately Atlantic waters, Southern Barents Sea (sub-Arctic-boreal)[g]
Average adult body size (total length, mm)	25[b]	42 (varies regionally)[e]	40 (max. 60)[h]	18[m]
Feeding strategy	Predominantly herbivorous, some observation of feeding on copepods[c]	Omnivorous, very flexible diet[c,f]	Carnivorous, feeding throughout the year[i]	Predominantly carnivorous, feeding throughout the year[i]
Reproductive strategy and breeding season	Capital breeding. Spawning-May to June[d]	Income breeding. Spawning-March to July[e]	Mixed breeding. Brooding- December to March, young released-February to May[j–l]	Mixed breeding. Brooding- December to March, young released-May to June[g,k,l]

Includes distribution within the Barents Sea, approximate adult size, feeding and reproductive strategy, regarding a capital-income approach and breeding season

[a]Dalpadado and Skjoldal (1991)

[b]Dalpadado and Skjoldal (1996)

[c]Schmidt (2010)

[d]Dalpadado and Skjoldal (1995)

[e]Tarling (2010)

[f]Pond et al. (2012)

[g]Dalpadado (2002)

[h]Auel and Werner (2003)

[i]Kraft et al. (2013)

[j]Percy (1993)

[k]Weslawski and Legeżyńska (2002)

[l]Kraft et al. (2015)

[m]Koszteyn et al. (1995)

weighing between 0.1 and 0.3 g (Table 2). Energy content (kJ g^{-1} dry weight) was measured for each pellet. Where possible, two replicate pellets of a single sample were run to ensure the calorimeter output was consistent. In some cases, more than two replicate pellets were run from a single sample (see data DOI for information regarding the number of replicates per sample). An average was taken of the replicates per sample (i.e. each sample produced a single calorimetric value), for use in further data analysis. Benzoic acid tablets (0.2 g) were used for calibration. Error margin for benzoic acid was $\pm 0.9\%$, while the error margin for biological material is slightly higher depending on homogeneity of the sample.

Data treatment and statistical analysis

Due to the unbalanced data set, the effects of season, species and size class were tested using a combination of Two-Way ANOVAs: To test for intra-specific differences in energy content from summer to winter, data were grouped by species and effects of season and size were estimated. To test for inter-specific differences, data were grouped by season and tested for the effect of species and size class on differences in energy content in both summer and winter. The effect of reproductive stage and size class on energy content was also tested for in winter *T. libellula* samples. Post-hoc Tukey's HSD tests were used where ANOVAs were significant (p value < 0.05). For statistical testing, the midpoint of the allocated size classes was used (i.e. 15 mm for the 10–20 mm class). All statistical testing was performed with R software (version 4.0.2) (R Core Team 2020).

Results

Intra-specific energy differences, based on seasons and size classes

The energy content of the krill *T. inermis* was similar from summer to winter (ANOVA, $F = 0.10$, $p = 0.76$ (Table 3;

Fig. 2a, b). The only seasonal energetic differences occurred when comparing different size classes, with the largest size class, 21–30 mm, having the highest energy content in both seasons (Tukey's HSD, both seasons $p < 0.001$) (Fig. 2c, d). For *M. norvegica*, the average energy content increased 8.3%, by 1.89 kJ g^{-1}, from summer to winter (ANOVA, $F = 14.36$, $p < 0.001$) (Table 3; Fig. 2a, b). However, there was no difference in the energy content between size classes (ANOVA, $F = 1.38$, $p = 0.27$) (Fig. 2c, d).

The amphipod species showed greater seasonal variation in energy content compared to the krill species. *T. libellula* showed the largest difference, from summer to winter, with a 18.6% decrease, of 4.3 kJ g^{-1}, whilst *T. abyssorum* saw a 15.6% decrease of 3.3 kJ g^{-1} (ANOVA, $F = 11.47$, $p = 0.001$ and $F = 9.44$, $p = 0.01$, respectively) (Table 3, Fig. 2a, b). The average energy content for *T. libellula* was higher in summer compared to winter across all size classes. Within both summer and winter, the energy content of *T. libellula* increased with size, from

11–20 to 31–40 mm (ANOVA, $F = 18.28$, $p < 0.001$), but remained similar in the 0–10 mm and 11–20 mm size classes (Tukey's HSD, $p = 0.73$) (Fig. 2c, d). For *T. abyssorum*, energy content did not differ between size classes within either season (ANOVA, $F = 0.79$, $p = 0.40$) (Fig. 2c, d).

Inter-specific energy differences in summer and winter

Summer

T. inermis had the highest energy content of all study species in summer, whilst *T. abyssorum* had the lowest (ANOVA, $F = 17.01$, $p < 0.001$) (Table 3). The Arctic counterpart in krill, *T. inermis*, had a higher energy content compared to the boreal *M. norvegica* (Tukey's HSD, $p < 0.001$), whilst both the amphipod species were similar in summer (Tukey's HSD, $p = 0.1$) (Fig. 2a). There was no difference in energy content between *M. norvegica* and both *T. libellula* and *T. abyssorum* (Tukey's HSD, $p = 0.95$ and $p = 0.39$, respectively) (Fig. 2a).
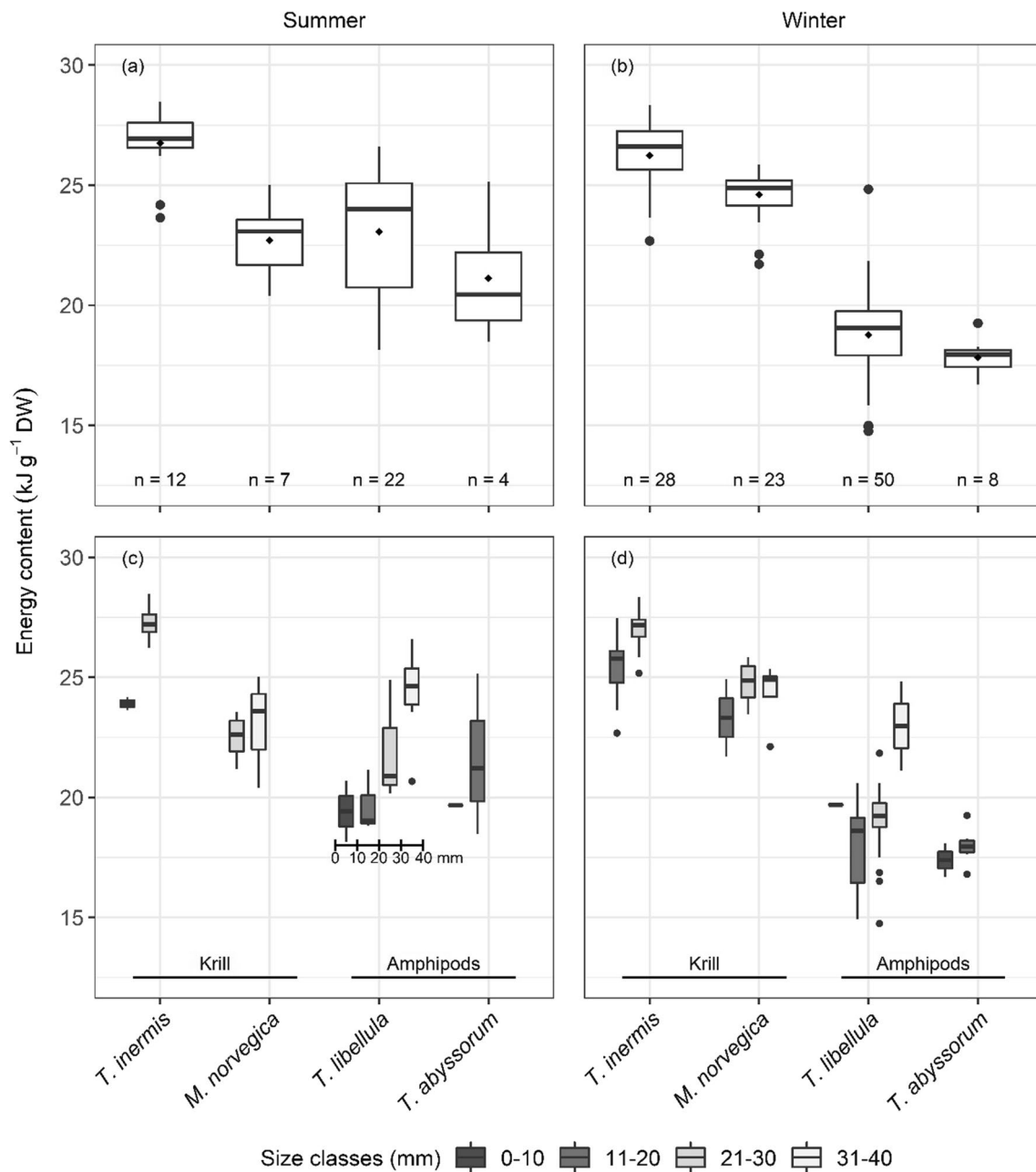
Winter

Differences in energy content between species were dependent on size class in winter, for all species (ANOVA, $F = 3.93$, $p = 0.005$). *T. inermis* in the 21–30 mm size class had the highest energy content compared to other study species and sizes (Tukey's HSD, ranging from $p = 0.001–0.04$, depending on species and size) (Fig. 2d). *T. abyssorum* had the overall lowest energy content in winter but was similar in value to the smaller size classes (0–30 mm) of *T. libellula* (Tukey's HSD, $p > 0.5$) (Fig. 2d).

Energetic differences between *T. libellula* reproductive stages in winter

In winter, the energy content of *T. libellula* varied depending on reproductive stage (ANOVA, $F = 6.72$, $p < 0.001$). The

Table 2 Overview table for the number of pellets (*n*) used in calorimetry, to determine energy content, for each study species, size class and season

Species	Size class (mm)	*n*	
		Summer	Winter
Thysanoessa inermis	11–20	2	14
	21–30	10	14
Meganyctiphanes norvegica	11–20	0	2
	21–30	4	17
	31–40	3	4
Themisto libellula	0–10	2	1
	11–20	3	20
	21–30	3	27
	31–40	14	2
Themisto abyssorum	0–10	1	2
	11–20	3	6

Krill and amphipods were collected from the Barents Sea in late summer and early winter

Table 3 Average seasonal energy content estimates for each species, in kJ g^{-1} of dry weight $\pm$ SD

	Summer			Winter		
	Energy content (kJ g^{-1} DW $\pm$ SD)	Mean size $\pm$ SD (mm)	*n*	Energy content (kJ g^{-1} DW $\pm$ SD)	Mean size $\pm$ SD (mm)	*n*
Thysanoessa inermis	26.75 $\pm$ 1.48	23.33 $\pm$ 3.89	12	26.24 $\pm$ 1.30	20.00 $\pm$ 5.09	28
Meganyctiphanes norvegica	22.71 $\pm$ 1.57	29.29 $\pm$ 5.35	7	24.60 $\pm$ 1.03	25.87 $\pm$ 5.15	23
Themisto libellula	23.07 $\pm$ 2.60	28.18 $\pm$ 10.41	22	18.77 $\pm$ 1.84	21.00 $\pm$ 6.06	50
Themisto abyssorum	21.13 $\pm$ 2.91	12.50 $\pm$ 5.00	4	17.83 $\pm$ 0.82	12.5 $\pm$ 4.63	8

Mean size for each species was calculated by taking the average of size class midpoints and should only be considered a rough estimation. *N* represents number of pellets used in calorimetry analysis per species per season

Fig. 2 Boxplots showing energy content (Energy content kJ g^{-1} dry weight (DW)) across species in **a** late summer and **b** early winter and the distribution of energy content across size classes in each species in **c** late summer and **d** early winter. Boxes represent the interquartile range (IQR), with the horizontal line representing the median and vertical bars representing range, up to $1.5 \times$ IQR. Points beyond these lines are considered outliers. In **a** and **b** the number of samples represented by each box plot is indicated by "$n=$", and diamonds inside boxes represent the mean

average energy content of gravid females was 2.57 kJ g^{-1} higher than males (Fig. 3a). The highest energy content was in a single 31–40 mm gravid female, at 24.9 kJ g^{-1}. Males had a lower energy content than both undetermined (Tukey HSD, $p = 0.01$) and gravid (Tukey HSD, $p = 0.006$) samples (Fig. 3a). Differences in energy content varied between size classes, with the 30–40 mm size class having higher energy contents than both the 11–20 mm (Tukey HSD, $p < 0.001$) and 21–30 mm (Tukey HSD, $p = 0.003$) size classes (Fig. 3b).
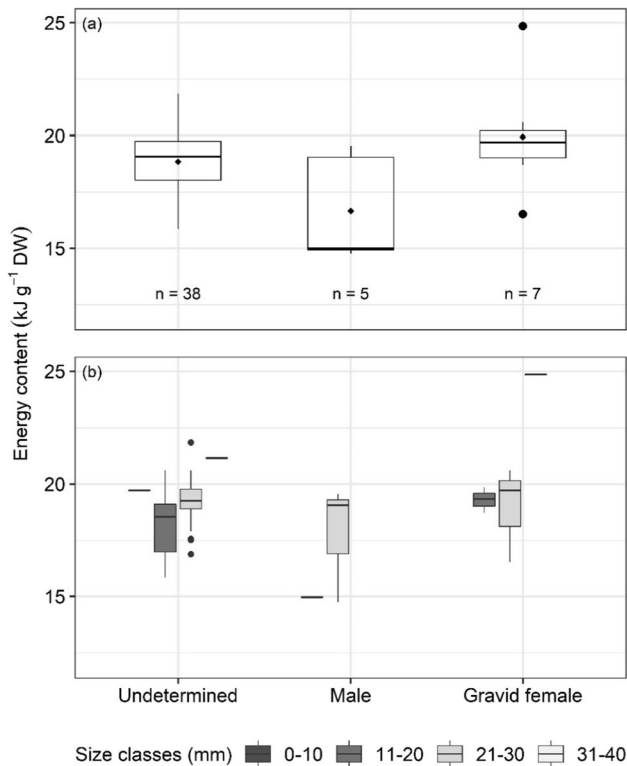
Fig. 3 Boxplot showing energy content (Energy content kJ g^{-1} dry weight (DW)) across **a** reproductive stages and **b** size classes, of winter *T. libellula* samples. Boxes represent the interquartile range (IQR), with the horizontal line representing the median and vertical bars representing range, up to 1.5 × IQR. Points beyond these lines are considered outliers. In panel **a** the number of samples represented by each box plot is indicated by "*n =*", and diamonds inside boxes represent the mean

Discussion

Energetics and feeding strategies

As expected, the highest energy content in both summer and winter was in the herbivorous Arctic krill, *T. inermis*. This species is known to have large lipid stores, primarily consisting of energy-rich wax esters (Falk-Petersen et al. 1981), a trait it shares with other predominantly herbivorous Arctic zooplankton, such as the copepods *Calanus hyperboreus* and *Calanus glacialis* (Hüenerlage et al. 2016; Cabrol et al. 2019a). Wax esters are associated with long-term energy storage in zooplankton (Lee et al. 2006). The relative stability in *T. inermis* energy content estimates coincide with the need to conserve energy throughout the winter, both to survive low food availability and fuel reproduction in the spring (Falk-Petersen et al. 2000). This conservation is achieved through a range of adaptations, such as sexual regression and negative growth, however metabolism through the winter is not reduced (Hüenerlage et al. 2015). There is also evidence

of some carnivory in *T. inermis* (Hüenerlage et al. 2015; Cabrol et al. 2019a), which could subsidize energy stores.

The Atlantic krill *M. norvegica* had a lower energy content than *T. inermis,* likely due to lower lipid content, as well as its primary storage lipid being triacylglycerol, which is less energy dense than wax esters (Falk-Petersen et al. 1981). Furthermore, triacylglycerol is associated with short-term storage in marine zooplankton (Lee et al. 2006), with *M. norvegica* likely relying on feeding throughout the year, compared to the stronger reliance *T. inermis* has on energy stores (Cabrol et al. 2019b). *M. norvegica* was the only species in our study to show an increase in energy content from summer to winter. Inhabiting an extensive geographic range, occurring across the north Atlantic and reaching south to the Mediterranean, *M. norvegica* shows great plasticity in its feeding depending on region and season (Schmidt 2010; Pond et al. 2012). In northern regions, this Atlantic krill shifts from a relatively herbivorous to a *Calanus* spp.-based diet in autumn (Båmstedt and Karlson 1998; Schmidt 2010; Cabrol et al. 2019a) which could explain higher winter energy contents that reflect preying on lipid rich copepods.

Contrastingly, the two amphipod species we studied showed lower energy content than either krill species, as well as a greater difference between summer and winter. These amphipods are known to be predominantly carnivorous, with less dependence on energy stores to withstand the non-productive period (Auel et al. 2002). Despite showing a large decrease in energy content from summer to winter, both amphipod species have been found to feed during the polar night in some Svalbard fjords (Kraft et al. 2013). However, more than half of the *Themisto* spp. guts sampled in Rijpfjorden, a fjord characterised by Arctic waters, were less than 25% full (Kraft et al. 2013), indicating that hunting during the dark winter months might be less effective for these predominantly visual predators. Although there will be differences between fjord and Barents Sea populations, this potentially less effective winter feeding may, in part, explain the decrease in energy content from summer to winter in *Themisto* spp.

Energetics, body size and life history strategies

There was a strong positive relationship between size and energy content for *T. inermis* and *T. libellula*. However, *M. norvegica* and *T. abyssorum*, did not show variation in energy content based on size. For *M. norvegica*, this was likely a result of small sample sizes per size class in summer, with no samples at all for the 11–20 mm size class (Table 2), therefore making it difficult to discuss ontogenetic energetic variation. For *T. abyssorum*, the lack of energetic variation with size may be due to applying size classes that were too broad for this small species, as *T. abyssorum* has a maximum size of about 18 mm (Koszteyn et al. 1995; Table 1).

The increase in energy content with size in *T. inermis* is likely due to reallocation of energy from growth to reproductive efforts upon reaching maturity. *T. inermis* spawns from May to June, fuelling reproduction with energy reserves (Dalpadado and Skjoldal 1995; Table 1). Therefore, the increase in energy content with increasing body size is likely a result of energy being allocated to reserves for reproduction in the spring, versus being used for growth (Dalpadado and Ikeda 1989; Falk-Petersen et al. 2000; Pinchuk and Hopcroft 2006). This dependence on building energy stores for reproduction aligns with the stability in the energy content from summer to winter seen in this krill species.

T. libellula showed the most pronounced energy increase with size. Thus, energy content, from small to large individuals, is likely driven by ontogenetic changes in energy allocation, from somatic growth to energy reserves, for survival and reproduction. Total lipids increase from juveniles to adults (Noyon et al. 2011), correlating with the increase in energy content we see with increasing size in our study. The observed decrease in energy content, from summer to winter, aligns with lipid content being seen to decrease from summer to winter in *T. abyssorum* and *T. libellula*, due to reproduction (Kraft et al. 2015). This suggests there is an increase in reproductive investment towards the winter, which aligns with a mixed breeding approach (Table 1). This is further supported by the presence of mature males and gravid females of *T. libellula* in winter samples and although sample sizes were small, there were some differences between these reproductive categories. *T. libellula* is a brooder, with females carrying developing eggs in a brood pouch until they are released as juveniles (Percy 1993). However, eggs were not removed from the brood pouch in the analysed females, and therefore the estimates from these female samples "retain" the energetic content allocated to reproduction, through lipid rich eggs. This is one explanation for the highest energy content in winter *T. libellula* samples being a 31–40 mm gravid female, as well as higher energy content in 11–20 mm gravid females compared to males. From a predator perspective, gravid females could offer a highly nutritious prey option compared to males.

Present understanding and energetics in a future Arctic

We summarised energy content estimates in the existing literature (Table 4), and here compare our estimates with previous works. Where seasons and body sizes were comparable, the energy content estimates between our study and previous studies were mostly similar (e.g. energy content for *T. libellula* in our study and Walkusz et al. 2012). Energetic variation between seasons and body sizes has been shown to some extent in previous studies, with varying degrees of resolution (Table 4). One caveat of the present study is its restriction to only two seasons, namely late summer and early winter. Many past studies focused only on a single season, or a few months, but some studies sampled over the course of a full year (e.g. Tyler 1973; Table 4). Although, compiling studies gives additional insight into seasonal variation, in some cases over almost the entire year (e.g. for *T. inermis*, Table 4).

However, lack of differentiation between size classes of the individuals used for calometric analyses, or in some cases complete lack of size determination, is a barrier to comparisons between studies. In such cases, it cannot be known if variation in energy content is due to seasonal differences, or simply differences in the size classes used for analyses. The present study has shown that size is an important factor in energy content variation, both within and between species, due to changes (i.e. in diet or developmental stage) occurring over an organism's annual and life cycle. More so, size is known to impact a predator´s choice of prey (Gill 2003). Therefore, energetic values for a range of size classes will improve our knowledge of the energy content of prey available to predators. Such size dependencies are amplified in visually searching predators that more easily detect large individuals, and in the Arctic, sea ice declines may provide a more beneficial light environment for such visual search (Langbehn and Varpe 2017). Future studies, with frequent seasonal sampling and a high resolution of size classes, would provide an important understanding of the energetic landscape available to predators over an annual cycle.

Energy content is another important factor in prey choice (Houston and McNamara 1999; Spitz et al. 2010b, 2012). For endothermic predators, such as seabirds and marine mammals, living costs and the resultant metabolisms are high. More so, they can experience periods of particularly high energy demands, such as when seabirds are feeding their chicks (Gabrielsen et al. 1987). Therefore, changes in prey quality, from energy-rich to energy poor, can have major consequences. Coined the "Junk-food hypothesis", the phenomena of changing prey quality, from high to low, resulting in adverse effects on predators, has been well-documented (Österblom et al. 2008). Studies have suggested that lack of energetically rich fish species has resulted in decreased body condition and population decline in stellar sea lions (*Eumetopias jubatus*) (Alverson 1992) and reduced breeding success in black-legged kittiwakes (*Rissa tridactyla*) and tufted puffins (*Fratercula cirrhata*) (Romano et al. 2006), cape gannets (*Morus capensis*) (Grémillet et al. 2008) and common guillemots (*Uria aalge*) (Wanless et al. 2005). These negative outcomes were all a result of changing prey composition, where there was a reduced availability of high-quality prey. In a future Arctic, changes in the species composition of prey items could end up impacting predators in similar ways.

Table 4 Overview of the existing literature that contains estimates for the energy content of the four species of macrozooplankton in this study

Species	Geographic region	Time of year	Size class: mean, range (mm) or life stage	Energy content: mean or range (kJg⁻¹ DW, unless otherwise noted)	References
Thysanoessa inermis	Bering Sea	(a) Apr-Jun, (b) Jun-Sept	(a) (8–22), (b) (14–24)	(a) 18.22–27.42*, (b) 28.96–32.13* (kJ g⁻¹ AFDW)	Harvey et al. (2012)
	Western sub-Arctic Pacific	(a) Jan-Mar, (b) Apr-Sept	Adult	(a) 8.1 ± 0.6, (b) 6.3 (kJ g⁻¹ WW ± SD)	Kooka et al. (2018)
	Kongsfjorden, Svalbard	July	Juvenile and Adult	25	Weslawski et al. (2000)
	Frobisher Bay, Canada	Aug-Sept	Not stated in study	(24.28–26)*	Percy and Fife (1981)
Meganyctiphanes norvegica	Kosterfjorden, Sweden	December	Not stated in study	(24.76–31.66)*	Norrbin and Båmstedt (1984)
	Bay of Fundy, Canada	August	Not stated in study	19.68*	Kulka and Corey (1982)
	Passamaquoddy Bay, Canada	(a) Feb-Dec, (b) Jan-Dec	Not stated in study	(a) 20.70*, (b) 21.10*	Tyler (1973)
Themisto libellula	Kongsfjorden, Svalbard	July	(6–8) and (12–14)	19.8	Weslawski et al. (2000)
	Kongsfjorden, Svalbard	August and March	23	16.71	Weslawski et al. (1994)
	Frobisher Bay, Canada	Aug-Sept	Not stated in study	(17.67–23.53)*	Percy and Fife (1981)
	Southern Barents Sea and Isfjorden, Svalbard	July	(11.1–12)	17	Weslawski et al. (1999)
	Beaufort Sea	August	16	19.99*	Walkusz et al. (2012)
	Hornsund, Svalbard	Jul–Sept	Not stated in study	13.64 ± 0.51 (± SD)	Wolowicz and Szaniawska (1986)
Themisto abyssorum	Kongsfjorden, Svalbard	July	Over 5	19.8	Weslawski et al. (2000)
	Southern Barents Sea and Isfjorden, Svalbard	July	(8.1–9)	18.4	Weslawski et al. (1999)
	Kosterfjorden, Sweden	April	Not stated in study	19.82*	Norrbin and Båmstedt (1984)
Thysanoessa spp.	Norwegian Sea and Barents Sea	Jan- Nov	Not stated in study	(2.3–8.2)ᵃ (kJ g⁻¹ WW)	Mårtensson et al. (1996)
Themisto spp.	Western sub-Arctic Pacific	(a) Jan-Mar, (b) Apr-Sept	Adult	(a) 4.4 ± 0.2, (b) 3.4 (kJ g⁻¹ WW ± SD)	Kooka et al. (2018)

Information is given regarding: Geographic region; Time of year for which the energy content estimates apply to, as stated in original study; Size class in terms of total length, as stated in original study for mean or range (given in parentheses) of lengths, or life stage where length wasn't stated; Energy content as mean or range (given in parentheses). Energy content is shown in kJ g⁻¹ of dry weight (DW), unless otherwise noted (i.e. Ash-free dry weight, AFDW; wet weight, WW). In some cases, original energy content estimates have been converted from calories to kilojoules to allow for better comparison across studies, indicated with an asterisk (*)

Like the rest of the Arctic, the Barents Sea is experiencing the effects of climate change at a faster rate and a greater magnitude than elsewhere on the planet, predominantly through increasing temperatures and reduced sea ice cover (CAFF 2017; Lind et al. 2018; AMAP 2021). This warming climate is leading to borealization, with sub-Arctic species of zooplankton and fish becoming more abundant in Arctic regions (Fossheim et al. 2015; Vihtakari et al. 2018). The present study shows that phylogenetically and morphologically similar prey items cannot necessarily be considered equal, and that feeding and reproductive strategies influence the energy content of prey. This is shown in the comparison of Arctic and Atlantic krill in the present study, whose energetic discrepancies are also seasonally dependent. Spitz et al. (2010b) categorised the energetic quality of prey (kJ g⁻¹ of wet weight (WW)) as follows: Low Quality (< 4 kJ g⁻¹), Moderate Quality (4–6 < kJ g⁻¹) and High Quality (> 6 kJ g⁻¹). For the 20–30 mm size class of *Thysanoessa inermis* and *Meganyctiphanes norvegica*, the average percentage dry weights (%DW) were then taken for each species.

The dry weight of the total sample was divided by the wet weight, for each species in each season. In some cases, the dry weight or wet weight had not been taken, and therefore these samples were excluded from the %DW calculation. The existing average energy content (kJ g^{-1} dry weight) for each species in each season was divided by the average %DW, to produce energy content estimates in kJ g^{-1} wet weight. When the summer and winter averages for *T. inermis* and *M. norvegica* in the size class 20–30 mm are converted into energy content based on wet weight, *T. inermis* can be considered a high-quality prey item in both summer and winter, 8.6 kJ g^{-1} (WW) and 8.3 kJ g^{-1} (WW), respectively. Contrastingly, *M. norvegica* shows an energy content almost half of its Arctic counterpart in summer, 4.5 kJ g^{-1} (WW), categorising it as moderate quality, and rising to a high-quality standard in winter, 6.6 kJ g^{-1} (WW). If *M. norvegica* were to replace *T. inermis* as a dominant prey item in Arctic waters, it would prove a lower quality replacement in the summertime.

Indeed, the complexity of prey energetics shown in this study needs to be fully realised, to make informed decisions on the sustainable development of Arctic marine ecosystems. The Norwegian Ministry of Climate and Environment (2006; referenced in 2020 report) explicitly states the need for "more knowledge about energy flow and interactions between species if we are to develop a sound management regime" in the *Integrated Management Plan for the Barents Sea*. The energy content estimates in the present study takes a step towards this understanding.

This study has shown that energy content, and hence the quality of prey, can vary seasonally and so cannot be considered a constant value over an annual cycle. More so, this study shows that energy content can vary between even seemingly similar species and is associated with traits related to feeding and energy storage. Size differences, within and across species, are also an important factor in the energy content. Realising the energetic variation of key prey species is paramount in our understanding of the functioning of Arctic marine ecosystems, particularly when considering the effects to higher trophic levels. Hence, the dynamics shown in this study should be considered when incorporating energetics into ecological models and management strategies.

Author contributions RN, KB, GWG and ØV contributed to study design and conception. RN conducted fieldwork, with help from ØV. RN conducted lab analysis. RN analysed the data, with supervision by ØV. RN wrote the manuscript, with feedback and contributions from KB, GWG and ØV. All authors read and approved the final manuscript.

Declarations

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