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Visser, Andre; Grønning, Josephine Bøgeskov; Jonasdottir, Sigrun

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Andre W. Visser,* Josephine Grønning, Sigrún Huld Jónasdóttir
VKR Centre for Ocean Life, National institute of Aquatic Resources, Technical University of Denmark, Kgs. Lyngby, Denmark

Abstract
Lipid-fuelled overwintering by copepods can be a regionally important contribution to carbon sequestration in the deep oceans. Here, we estimate the contribution for *Calanus hyperboreus*, found in abundance in the northern reaches of the North Atlantic and Arctic Ocean. Estimates for regions with high overwintering populations, Fram Strait, Greenland Sea and Iceland Sea lie between 3.5 gC m^{-2} yr^{-1} and 6.0 gC m^{-2} yr^{-1} at depths of 1000–3000 m, comparable to the flux of detrital organic carbon at commensurate depths. Apart from the variation in the abundance of overwintering populations, these estimates are most sensitive to mortality rates. We present a general model based on metabolic theory and isomorphism that can be used to constrain estimates for data poor species in other parts of the global ocean.

In various parts of the world's oceans, large populations of zooplankton undertake seasonal migrations to depths of a 1000 m or more where they overwinter for several months of the year. These seasonal migrations have been identified as a potentially significant element of the biological pump, promoting the sequestration of carbon in the deep ocean (Bradford-Grieve et al. 2001; Kobari et al. 2008; Jónasdóttir et al. 2015). An important aspect of this is the active transport of stored lipids by individual zooplankters as they migrate from the surface ocean to their overwintering depths below the permanent thermocline. These stored lipids subsequently fuel respiration during winter. Even with markedly lower metabolic rates, the extended periods spent at depth, means that a significant fraction of the transported lipids are converted to CO_2, and remain at depth after the individual returns to the surface the following spring. For *Calanus finmarchicus*, a copepod species found in abundance across the North Atlantic, this process—the so called lipid pump (Jónasdóttir et al. 2015)—can constitute a substantial contribution to the local carbon flux. An important feature of lipid-fuelled overwintering is that unlike the flux of detrital material, it transports carbon directly to the deep ocean with very little loss on the way. In addition, it decouples the vertical flux of carbon from that of the main limiting nutrients for primary production (e.g., nitrogen, phosphorus, iron). This makes the lipid pump not only particularly efficient in carbon sequestration, it also make it difficult to document

(Jónasdóttir et al. 2015) as it leaves little trace in the nutrient budgets of the surface ocean.

A full global accounting of the lipid pump thus remains elusive as it depends on the abundance of a wide variety of resident zooplankton species often with quite varied life history strategies. Ecologically similar species such as *Calanus hyperboreus* in the Nordic Seas (Conover 1992; Hirche 1997), *Neocalanus tonus*, *Calanoides acutus*, *Rhincalanus gigas*, and *Calanus propinquus* in the Southern Ocean (Bathmann et al. 1993; Atkinson 1998; Bradford-Grieve et al. 2001), *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the North Pacific (Miller et al. 1984; Kobari et al. 2008), and *Calanoides carinatus* and *Eucalanus monachus* in the Indian Ocean (Smith 1995) are all candidate species in that they engage in lipid-fuelled diapause in deep ocean basins. While this list is by no means exhaustive, it does illustrate the challenge of compiling a global inventory.

Our primary motive here is to document the contribution from one of these, *C. hyperboreus* in the North Atlantic and adjacent Seas. The method we use is cast in a general manner that can serve template for other species in other regions of the global ocean. In particular, we appeal to the metabolic theory of ecology (Brown et al. 2004) which can provide estimates of important vital rates and processes that may be poorly constrained by observations. Specifically, respiration rates for overwintering individuals can be estimated from a few observations and extended across different temperatures, different sized species and life stages. Respiration rates can also constrain the length of diapause given observations of lipid reserves (Saumweber and Durbin 2006; Maps et al. 2010; Pierson et al. 2013).

In general, estimates of the sequestered carbon by seasonal migration are based on the difference between how much

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*Correspondence: awv@aqua.dtu.dk

is transported down in the late summer, and how much comes back to the surface in spring. This depends on the stage specific abundances of the of overwintering individuals, their respiration integrated over their respective overwintering durations, corrected for the mortality of individuals at depth, especially spent females, and discounted for the eggs spawned at depth that return to the surface in spring. Different aspects of this carbon budget become important for different species in different regions. For instance, *N. tonus* in the Southern Ocean has a 1 yr life cycle where the copepodite stage CV overwinters, molts into an adult, spawns and then expires at depth (Ohman et al. 1989). In this case, while details of respiration and mortality may be sketchy, the net carbon flux can be relatively easily closed as being essentially the difference between the active downward transport by migrating CV's and the upward drift of eggs the following spring (Bradford-Grieve et al. 2001). In other instances such as for *C. finmarchicus* in the North Atlantic, females return to the surface to spawn, so that overwintering duration and respiration rate become important governing factors. The life history strategy of *C. hyperboreus*, includes elements of both these cases, and requires estimates of deep water egg production, mortality and respiration for a full evaluation of its overwintering carbon budget. The *C. hyperboreus* case thus presents an ideal opportunity to outline general principles for estimating carbon sequestration by seasonally migrating zooplankton.

Methods

Compilation of *C. hyperboreus* observations

Along with its cousin species *C. finmarchicus*, *Calanus glacialis* and *Calanus helgolandicus*, *C. hyperboreus* plays a key role in the ecology of the North Atlantic. *C. hyperboreus* is the largest of these species. Through its life history strategy combining both capital breeding and overwintering diapause, it is well adapted to the strong seasonal pulsing of food availability in the boreal reaches of the North Atlantic and adjacent seas. It is particularly abundant—in terms of biomass—in the deep basins of the Nordic Seas, Greenland Basin and Iceland Sea, while its smaller cousin, *C. glacialis* occupies the shallower shelf sea zones of these regions.

C. hyperboreus has a multi-year (2–6 yr) life cycle. Females spawn lipid rich eggs at depth that are positively buoyant and drift toward the surface (Hirche and Niehoff 1996; Swalethorp et al. 2011) where they develop into nauplii. Its maturation through naupliar stages to an early copepodite stage is completed within one season after which it overwinters as a CIII or CIV (Falk-Petersen et al. 2009). The development rate and subsequent ontogeny of overwintering varies from place to place likely in response to the intensity and duration of the vernal bloom, as well as individual plasticity in the allocation of resources to somatic growth or lipid reserves. A typical sequence would have an individual

overwinter 3–4 times, as a CIII, CIV, CV, and adult. There are no clear reports of what happens to the females after spawning. It is generally understood that spent adults expire at depth, however observations of spent *C. hyperboreus* females in surface waters in spring suggests that at least some fraction may ascend, feed and build up lipid stores again and go through a second overwintering and reproduction cycle (Swalethorp et al. 2011; Hirche 2013).

The overwintering stages (CIII, CIV, CV, and adult) all store the lipids in the form of wax esters in an internal oil sac. The oil sac can occupy a considerable fraction of the internal volume, and can constitute up to 60% of the total dry weight of individuals across all stages. *C. hyperboreus* overwinters typically at depths between 600 m and 3000 m (Hirche 1997; Falk-Petersen et al. 2009), although, overwintering depths vary depending on location, ontogeny, and season. In some instances, overwintering populations appear to reside in a relatively thin layer a few tens of meters thick just above the seabed at some 1000s m depth (Auel et al. 2003; Hirche et al. 2006).

Distribution, abundance and stage composition of *C. hyperboreus* was attained through data mining of most of the available literature. Data from over 50 papers were compiled standardizing abundances to numbers per m^2. If numerical data were not presented we used the image processing programme Image-J (Abràmoff et al. 2004) for reading abundances and station locations from graphs and maps. We refer to the Supporting Information material for a complete list of publications from which data has been extracted for this analysis, as well as a compilation of these observations. For the calculation of carbon sequestration we restricted the use of data from locations over 600 m in depth as sequestration will not take place on shallow overwintering areas.

Model

The sequestering of carbon by *C. hyperboreus*, and indeed for many of the other species that can potentially contribute to the lipid pump, depends on several parameters that are only poorly constrained. For instance, respiration rate during diapause has been measured only for a few species (Hirche 1997; Ingvarsdóttir et al. 1999; Auel et al. 2003) and then only in specific locations and after the animals have been brought to surface. Likewise, the regular winter surveys required to map out the depth and duration of diapause have only been conducted in a few cases, e.g., *C. finmarchicus* (Heath et al. 2000). In this, we can appeal to metabolic theory to help fill in the knowledge gaps. In particular, the thermal and allometric aspects of metabolic rates appear to follow a near universal functional form. Keiber's law (Kleiber 1947) for instance suggests that the metabolic rate of an organism scales as a ¾ power of its mass. In addition, metabolic rates tend to increase with temperature (Arrhenius 1889) providing a thermo-allometric relationship

$$r(M,T) = b \cdot M^{3/4} \exp\left(E \cdot (T-T_0)/(k \cdot T \cdot T_0)\right) \qquad (1)$$

where M [μgC] is mass, r [μgC s^{-1}] is respiration rate, T [K] is temperature, b [μgC$^{1/4}$ s^{-1}] is a universal scaling constant, E [eV] is the activation energy and k [eV K^{-1}] the Boltzmann constant. T_0 is a base temperature, usually taken as $T_0 = 273$ K. The metabolic theory of ecology (Brown et al. 2004) provides a theoretical foundation for this relationship and it is fairly well supported by observations for life forms in their natural thermal range, from unicellular organisms, to vascular plants to bird, fish and mammals (Gillooly et al. 2001). When applied within taxa (e.g., Calanoid copepods), the fit is even more robust (Kiørboe and Hirst 2014).

In applying this scaling to an overwintering copepod, we should distinguish between two different types of mass; its vital (or structural) mass m and its mass of stored lipid reserves w. Notably, while Eq. 1 relates metabolic rate to total mass ($M = m + w$), one could reasonably assume that base metabolism is largely dependent only on vital mass, while the fuel to cover this metabolism comes largely from lipid reserves mass. This suggests a linear decrease in lipid mass over time that follows

$$w(t) = w(0) - b \cdot f(T) \cdot m^{3/4} \cdot t \qquad (2)$$

where f is a dimensionless function depending only on temperature. Note that this is a departure from other model frameworks (Saumweber and Durbin 2006; Maps et al. 2014) who do not make the distinction between vital and storage mass and thus arrive at an exponential decay of total mass with time. While this does not invalidate these analyses—the exponential decay can be extremely flat approximating a linear decrease over the range of interest—it does make the subsequent interpretation overly cumbersome and difficult to extrapolate across species and stages.

Given their shared evolutionary history, one might expect that metabolic rate for various copepod species in diapause to be governed by a similar thermo-allometric scaling law. A review (Maps et al. 2014) of measured metabolic rates for dormant copepods across the global ocean provides estimates of $b = (2.3 \pm 0.4) \times 10^{-7}$ μgC$^{1/4}$ s^{-1} and activation energy $E = 0.6 \pm 0.1$ eV.

The physical characteristics of *C. hyperboreus* (i.e., prosome length, dry weight, carbon content, lipid content) all vary considerably from place to place and over time of year as well as across life stages. In order to uncover some relatively general principles, we appeal to isomorphism: that is, across different overwintering stages and even between different pelagic copepod species, individuals may vary in size but their basic physical design remains remarkably constant (Kiørboe 2008). In *C. hyperboreus* for instance, apart from size, the only significant taxonomic difference across stages CIII–CV is the number of segments on the tail. An outcome of isomorphism is that any physical characteristic such as

structural mass would scale with the cube of any linear dimension. For instance, all things being equal, dry weight (d [mg]) and prosome length (p [mm]) should be related as $d = c\,p^3$.

Such a relationship is at first glance not supported by empirical evidence. Observations from the Arctic (Hirche and Mumm 1992) show a power law relationship between prosome length and dry weight with a coefficient between 3.3 and 3.5 for *C. hyperboreus* from stage CIII to females (Fig. 2). While establishing the exact form of a power law is in itself notoriously difficult, we contend that there is a systematic bias in observations that will tend to steepen the power law fit. In Fig. 2, we also plot the wax ester content (based on oil sac area) drawn from observations in the Labrador, Irminger, Iceland and Greenland Seas. In all observed individuals, wax ester content can constitute a significant fraction of the dry weight—from 60% to 20%, and a scaling law regression fit shows a similar power law relationship with prosome length as dry weight. The sampling bias comes about because smaller stages deplete their reserves to relatively lower levels (e.g., from 60% to 20% over a winter season) than larger animals (e.g., 60% to only 40% over the same period). Sampling at any given time would tend turn up more depleted small organisms than large animals. The only way to circumvent this bias is to measure the weight and lipid content of individuals at precise milestones in their life cycle—immediately after they emerge from diapause before they start to feed, or immediately before they descend to depth at the end of the growing season. Indeed, one study that seeks to describe seasonal variations in allometric carbon content (Forest et al. 2011) suggests a relationship more in line with a cubic power law (i.e., consistent with isomorphic scaling), although this is by no means conclusive.

We propose the following model, founded on the principle of isomorphism, as a parsimonious alternative that conforms to observations and that can find a broader application for other data poor species. First, there is a basic body plan by which structural (vital) mass (m [μgC]) scales with prosome length:

$$m = \alpha p^3 \qquad (3)$$

Second, there is a potential maximum and minimum reserve (wax ester) mass [μgC] respectively given by

$$w_{\max} = \beta p^3$$
$$w_{\min} = \delta \beta p^3 \qquad (4)$$

Thus the observed wax ester content (ω [μg]) would lie between $\beta\,p^3/\varepsilon$ and $\delta\,\beta\,p^3/\varepsilon$ where ε is the carbon fraction of wax ester mass. Using $\varepsilon = 0.8$ (calculated from Kattner and Hagen 2009), a reasonable fit for observations (Fig. 2) is given by $\beta = 7.2$ [μgC mm^{-3}] and $\delta = 0.2$. Similarly, total dry

mass (d [μg]) would lie between $(\alpha/\varepsilon' + \beta/\varepsilon)\, p^3$ and $(\alpha/\varepsilon' + \delta\beta/\varepsilon)\, p^3$ where $\varepsilon' = 0.7$ is the carbon fraction of structural mass. Again a reasonable fit is given by $\alpha = 4.2$ [μgC mm^{-3}].

It has been suggested that the emergence from diapause is initiated when the reserve levels reach a critical percentage of the overall body mass (Saumweber and Durbin 2006; Maps et al. 2010). Given the above scaling, this would give an estimate of diapause length as

$$D_i = \min\left(\frac{(1-\delta)w_{i,\max}}{bf(T)m_i^{3/4}}, D_{\max}\right) \tag{5}$$

where the subscript i indicates different values for different stages. $D_{\max}$ is a maximum diapause duration, chosen to be representative of particular populations. In effect, this means that large stages do not deplete their resources to the same level as smaller stages, or, if they do, then small stages remain in diapause for a shorter period than larger stages. For *C. hyperboreus*, the diapause duration of all stages appears to be at least 8 months (Hirche 1997) in various locations across the Arctic Ocean and Nordic Seas, with some observations suggesting diapause duration of up to 10 months. For the purposes of this work, we set $D_{\max} = 240$ d.

For specific respiration rate, we choose two representative values of b; 2.5×10^{-7} and 5×10^{-7} μgC$^{1/4}$ s^{-1}. The latter of these ($b = 5 \times 10^{-7}$ μgC$^{1/4}$ s^{-1}) correspond to the value reported by Maps et al. (2014), duly multiplied by the factor $(1 + w_{\max}/m)^{3/4}$ to account for our use of structural mass rather than total mass in allometric scaling, and assuming the measured animals had maximum lipid reserves. This value of b however allows for only relatively short diapause duration—7 months for females and only 3 months for CIII—significantly less than observed (Hirche 1997).

To contrast this, we also consider a lower metabolic rate ($b = 2.5 \times 10^{-7}$ μgC$^{1/4}$ s^{-1}), a value which reproduces diapause duration close to observed, and results in a respiration rate of about 4 μgC d^{-1} for females consistent with the lower of the values reported by Auel et al. (2003). It is also consistent with the value reported by Maps et al. (2014) when scaled by $(1 + w_{\min}/m)^{3/4}$, i.e., assuming the measured animals had minimum lipid reserves.

The number of eggs produced by a female at the end of diapause is not easily measured. With no better information, we assume a female allocates $C_{egg} = 900$ μgC to egg production at depth. This is based on laboratory studies (Conover 1967; Hirche and Niehoff 1996; Plourde et al. 2003; Halvorsen 2015) which suggest an annual egg production of around 1800 (range: 400–3400) per female, and an egg carbon content of around 0.5 μgC (Jung-Madsen et al. 2013).

In addition to respiration, overwintering individuals also suffer mortality, whether from starvation, predation or pathogens (Daase et al. 2014). These rates, particularly in deep overwintering populations are poorly constrained. In this, we appeal to estimates for ecologically similar species

E. bungii which during diapause in the North Pacific show a wide range from 0.01 d^{-1} to 0.001 d^{-1} (Tsuda et al. 2004).

An estimate of annual carbon flux to depth, Q [gC m^{-2} yr^{-1}] can be calculated as the sum of respiration, mortality and egg production following

$$Q = \sum_{\text{stage}} A_i \frac{(1-e^{-\mu_i D_i})}{\mu_i D_i} r_i D_i + \sum_{\text{stage}} A_i(1-e^{-\mu_i D_i})\left(m_i + w_{i,\max} - r_i D_i/2\right)$$
$$+ \xi A_{\text{F}} e^{-\mu_{\text{F}} D_{\text{F}}}\left(m_{\text{F}} + w_{\text{F,max}} - r_{\text{F}} D_{\text{F}} - C_{egg}\right) \tag{6}$$

Here, A_i is the abundance [ind m^{-2}] of the various stages of an overwintering population that initially descend at the start of the overwintering period, μ_i its mortality rate, D_i its overwintering duration (Eq. 5), and r_i its respiration rate during diapause (cf Supporting Information material). The second term represents the contribution from mortality and in the third term, the factor ξ represents the fraction of females that expire at depth after spawning.

Finally, we note that the measured abundances are more representative of the average number of individuals $\bar{A}_i$ found at depth than they are of initial values A_i. Indeed, where multiple observations have been taken during diapause, we have expressly taken the average of these. Given a specific mortality rate, we can relate average and initial estimates as

$$\bar{A}_i = A_i \frac{(1-e^{-\mu_i D_i})}{\mu_i D_i} \tag{7}$$

so that in terms of average abundances, the flux is given by

$$Q = \sum_{\text{stage}} \bar{A}_i r_i D_i + \sum_{\text{stage}} \bar{A}_i \mu_i D_i\left(m_i + w_{i,\max} - r_i D_i/2\right)$$
$$+ \xi \bar{A}_{\text{F}} \frac{\mu_{\text{F}} D_{\text{F}} e^{-\mu_{\text{F}} D_{\text{F}}}}{1 - e^{-\mu_{\text{F}} D_{\text{F}}}}\left(m_{\text{F}} + w_{\text{F,max}} - r_{\text{F}} D_{\text{F}} - C_{egg}\right) \tag{8}$$

Results

The meta analysis resulted in three types of distribution information on *C. hyperboreus*, (1) total abundance, (2) stage composition and abundance and (3) studies reporting only presence (Fig. 1). We could use eight regions where information on abundance and stage composition during overwintering were sufficient for our analysis. These include Nansen Basin, Iceland Sea, West Spitzbergen Current, Greenland Sea, Fram Strait, East Norwegian Sea, West Norwegian Sea, and the Norwegian Sea Basin (Table 1). The stage composition is the average winter composition in the areas (October–February), compiled from the sampling depths available, preferentially over 600 m depth. We refer to Supporting Information material for the complete compilation of yearly and seasonal abundances and stage structure over the different oceanic regions (Supporting Information Tables S1–3; Supporting Information Fig. S1).
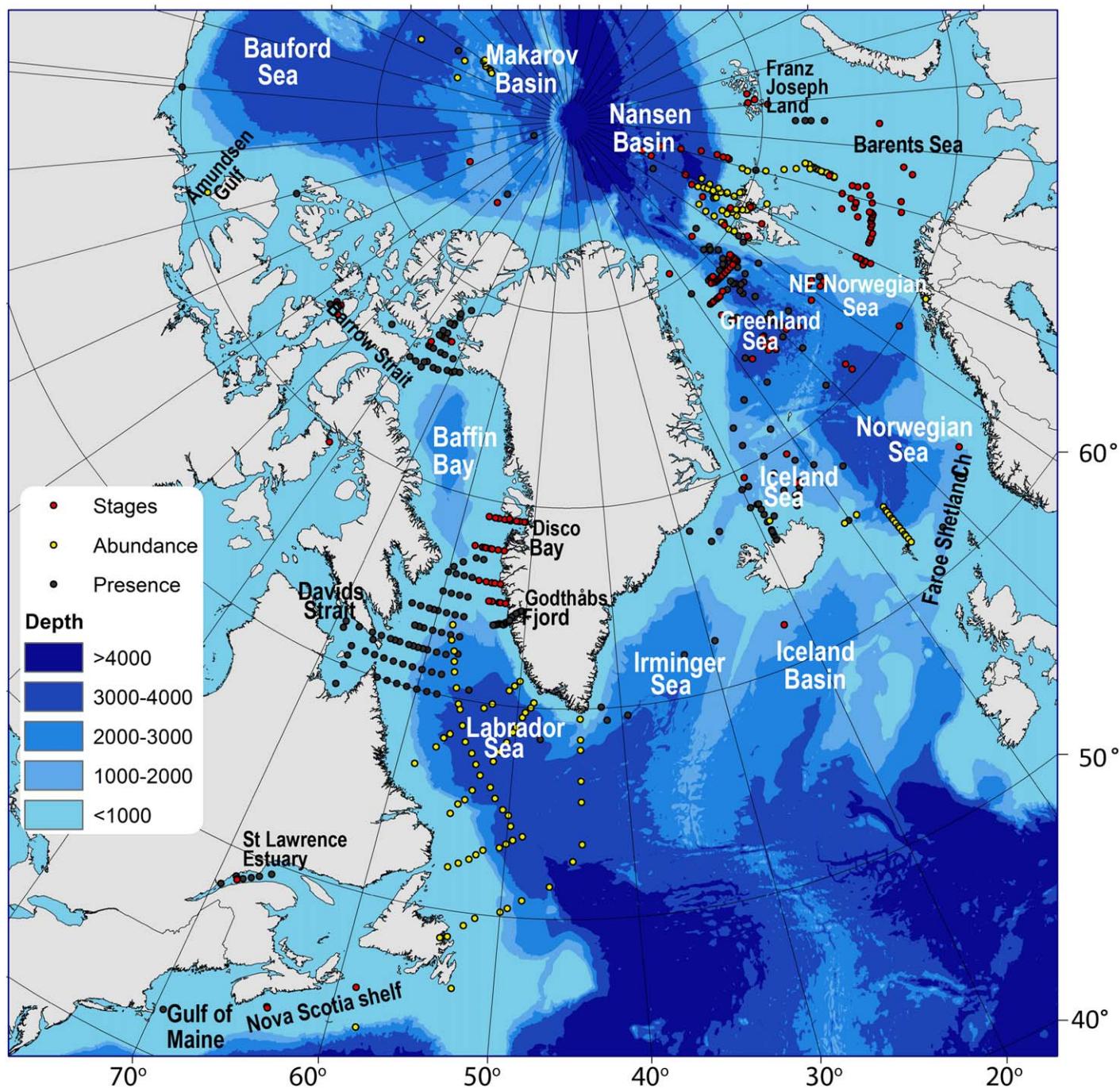
Fig. 1. *C. hyperboreus* distribution based on published sampling and notations of presence. Different symbols indicate stations giving stage abundances (Stages), abundance only (Abundances) and sampling without reporting on abundances (Presence). Source of the compilation is detailed in the Supporting Information Tables S1–S3. [Color figure can be viewed at wileyonlinelibrary.com]

Model results for the eight regions are summarized in Fig. 2. Estimated respiration rates for individuals range between 0.4 μgC d^{-1} and 4.0 μgC d^{-1} depending on stage and temperature. These estimates are consistent with some of the very few observations showing dormant *C. hyperboreus* CV and females respiring at 4–8 μgC d^{-1} (Auel et al. 2003). Using the

conservative lower metabolic rate estimate, ($b = 2.5 \times 10^{-7}$ μgC$^{1/4}$ s^{-1}), maximum assumed overwintering duration (D_{max}) of 8 months is achieved in all locations except for CIII stage which can only remain in diapause for around 7 months assuming a minimum wax ester reserve level of 20%, consistent with field observations (Hirche 1997). Integrating

Table 1. Depth, temperature, and abundance of overwintering *C. hyperboreus* in various regions of the Nordic Seas and Arctic Ocean; AB: Amundsen Gulf, AG (Forest et al. 2011): Nansen Basin (Daase and Eiane 2007), FS: Fram Strait (Auel et al. 2003), GS: Greenland Sea (Hirche 1997), WSC: west Spitzbergen Current (Hirche 1997), IS: Iceland Sea (Gislason and Astthorsson 1998), ENS: east Norwegian Sea (Edvardsen et al. 2006), WNS: west Norwegian Sea (Gislason and Astthorsson 2002; Kristiansen et al. 2016 using stage composition from Gislason and Astthorsson 1998), NS: Station M in the Norwegian Sea (Østvedt 1955) (cf. Fig. 1). Details of the calculations can be found in Supporting Information material. Flux associated with spent female a) lipid content carbon b) structural carbon assuming 50% females die at depth. See Supporting Information spread sheet for further details.

|		NB	FS	GS	WSC	IS	ENS	WNS	NS	AG
Overwintering depth [m]		1100	2000	500–3000	1000–3000	600–>1800	>900	1000	2000	>500
Temperature [°C]		−0.8	−0.8	−1	−1.2	−0.5	−0.5	0	−0.5	1
Abundance [m^{-2}] (range)	CIII	128 (111–145)	1048	6182 (1804–10683)	54 (8–104)	773 (657–890)	238 (120–306)	176	482 (273–2317)	188 (55–267)
	CIV	1011 (111–1910)	2749	3040 (2999–3449)	265 (8–404)	2273 (2131–2415)	441 (297–588)	335	528 (183–1594)	1061 (507–1638)
	CV	927 (170–1910)	2373	977 (556–2180)	115 (20–234)	1640 (1247–2034)	527 (412–618)	260	295 (68–822)	399 (224–1047)
	CF	208 (22–539)	775	924 (451–1171)	68 (12–121)	1137 (965–1209)	521 (371–705)	55	130 (20–462)	1251 (1064–1333)
	M	–	–	154 (0–310)	–	103 (0–205)	114 (97–138)	–	7 (0–28)	49 (0–121)
Total abundance: [m^{-2}]	CIII	2350	6946	11500	500	7196	1850	1400	1690	2948
Respired carbon [gC m^{-2} yr^{-1}]	CIII	0.01	0.09	0.56	0.00	0.07	0.02	0.02	0.09	0.02
	CIV	0.27	0.74	0.80	0.07	0.63	0.12	0.10	0.20	0.31
	CV	0.61	1.55	0.63	0.07	1.10	0.35	0.18	0.28	0.31
	CF	0.20	0.74	0.86	0.06	1.11	0.51	0.06	0.21	0.41
Total respired carbon [gC m^{-2} yr^{-1}]		1.10	3.17	2.91	0.21	2.97	1.03	0.35	0.78	2.04
Mortality at depth [gC m^{-2} yr^{-1}]	a)	0.01	0.04	0.06	0.00	0.05	0.02	0.00	0.01	0.00
	b)	0.12	0.45	0.53	0.04	0.66	0.30	0.03	0.12	0.72
Overall sequestration [gC m^{-2} yr^{-1}]		1.22	3.62	3.44	0.25	3.62	1.33	0.39	0.90	2.76
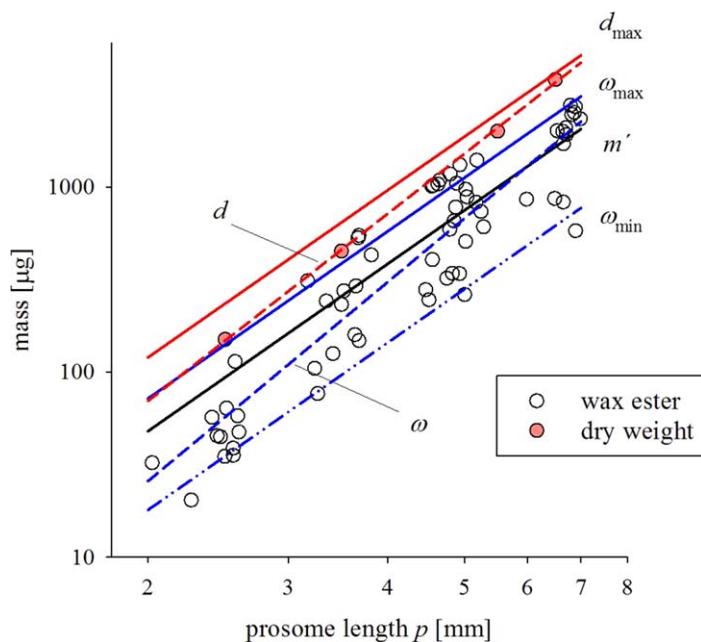
Fig. 2. Dry mass (d [μg]) and wax ester content (ω [μg]) as functions of prosome length (p [mm]) across stages CIII–CF for *C. hyperboreus*. Dry mass are averaged literature estimates (Hirche 1997; Scott et al. 2000; Auel et al. 2003; Falk-Petersen et al. 2009) while wax ester content are our own observations. Power law regressions to observations suggest $d = 6.79\ p^{3.36}$ and $\omega = 2.17\ p^{3.57}$ ($R^2 = 0.86$). Superimposed are our estimates of the maximum and minimum wax ester content $\omega_{max} = (\beta/\varepsilon)\ p^3$ and $\omega_{min} = (\delta\beta/\varepsilon)\ p^3$ respectively, and vital mass $m' = (\alpha/\varepsilon')\ p^3$ based on isometric scaling, with parameters $\alpha = 4.2\ \mu$gC mm^{-3}, $\beta = 7.2\ \mu$gC mm^{-3} and $\delta = 0.2$, and for a lipid mass carbon content of $\varepsilon = 0.8$ [μgC/μg] and a vital mass carbon content of $\varepsilon' = 0.7$ [μgC/μg]. [Color figure can be viewed at wileyonlinelibrary.com]

respiration rate over diapause duration and average abundance of the various overwintering stages gives estimates of respired carbon ranging as high as 3.1 gC m^{-2} yr^{-1}, a complete breakdown of the various contributions to the carbon flux, as well as estimates for the higher metabolic rate constant can be found in the Supporting Information material.

The other component of carbon sequestration comes about by mortality, for which there are two principle sources: general mortality during the entire diapause period, and the mortality of spent females at depth after spawning. Assuming half the female population dies after spawning (i.e., $\xi = 0.5$) increases the carbon sequestration estimate by about 30%. Most of this extra sequestration comes from the structural mass of the spent females since their reserve mass has been discounted for egg production. Including mortality during the diapause period, even at a very low rate of 0.001 d^{-1} for all stages, considerably increases the total carbon flux by a factor of about 80% over respiration alone. The overall flux thus ranges as high as between 3.6 gC m^{-2} yr^{-1} (for $\mu_i = 0$ d^{-1}) and 5.3 gC m^{-2} yr^{-1} (for $\mu_i = 0.001$ d^{-1}). A similar set of estimates, but for the higher value of b, range

between 4.8 gC m^{-2} yr^{-1} (for $\mu_i = 0$ d^{-1}) and 5.9 gC m^{-2} yr^{-1} (for $\mu_i = 0.001$ d^{-1}).

There are significant regional variations in these flux estimates. The highest values are observed in the eastern regions of the Nordic Seas (Fram Strait, Greenland Sea and Iceland Sea), all with flux estimates in the range 3–6 gC m^{-2} yr^{-1}. Flux estimates in the Norwegian Sea and Arctic Ocean are considerably lower with flux estimates of about 1 gC m^{-2} yr^{-1} or less. As might be expected, the greatest factor affecting these regional differences is the abundances of overwintering populations, ranging from 500 overwintering individuals for the lowest sequestration estimates to well over 10,000 overwintering individuals for the highest.

Discussion

The rain of detrital organic material out of the surface ocean is understood to be one of the main vehicles of the biological pump. The global average of the flux of this material that reaches depths of around 1000 m can be roughly estimated as 2–8 gC m^{-2} yr^{-1}, and is the fraction that can be considered as sequestered; i.e., removed from contact with the atmosphere for about a 1000 yr or so. These estimates are largely based on net annual surface productivity, usually constrained by nutrient budgets, and direct flux measurements by sediment traps. Growing evidence suggests that significant contributions to carbon sequestration are being supplied by overwintering populations of copepods in various parts of the global ocean. For instance, *Neocalanus tonsus* has been estimated to contribute between 2 gC m^{-2} yr^{-1} and 9 gC m^{-2} yr^{-1} to sequestration in the Southern Ocean (Bradford-Grieve et al. 2001) while the combined contribution from *Neocalanus* copepods in the Pacific subarctic has been estimated at between 2 gC m^{-2} yr^{-1} and 4 gC m^{-2} yr^{-1} (Kobari et al. 2003, 2008). Our estimates of 3–5 gC m^{-2} yr^{-1} for *C. hyperboreus* in the Nordic Seas also compares to our previous estimates of 1–4 gC m^{-2} yr^{-1} for *C. finmarchicus* in the more southerly reaches of the subarctic North Atlantic. For all of these estimates, a significant fraction of the sequestered carbon, whether through respiration or mortality, leaves the surface in the form of lipids—what we call the lipid pump. Since these lipids contain none of the limiting nutrients for surface primary production, and migrating copepods largely avoid sediment traps, contributions from the lipid pump are not included in previous estimates of the biological pump. There is clearly a case to be made that overwintering copepods are significant contributors to oceanic carbon sequestration, that this is a global phenomenon, and that this process has not as yet been accounted for in global carbon budgets.

In our current work, we have relied on a long history of studies into the distribution and abundance of overwintering populations of *C. hyperboreus*. Such observations are hard to come by given the season, the remote locations and the
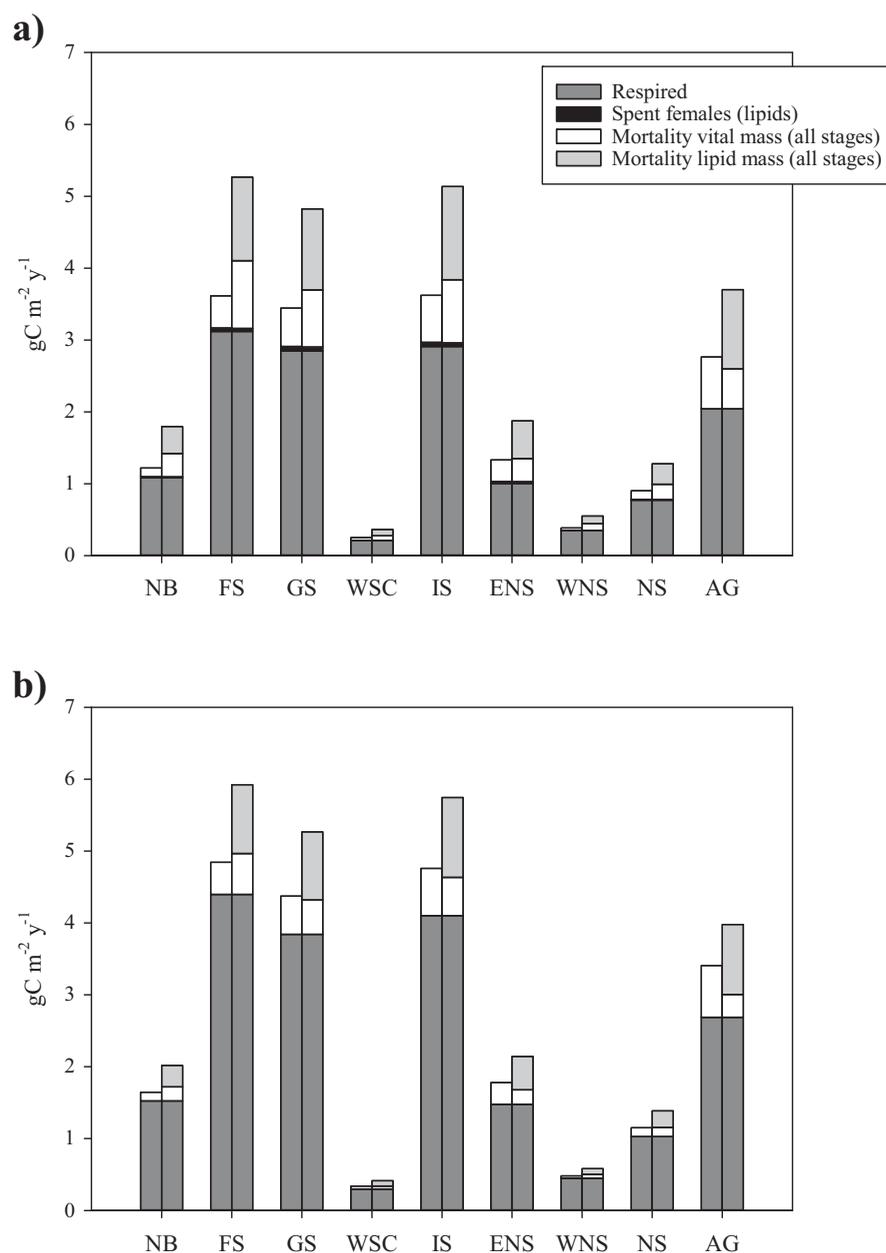
Fig. 3. Regional estimates of the carbon flux associated with overwintering populations of *C. hyperboreus*. Estimates are broken down as to respired flux, mortality flux of spent females lipid mass, mortality structural mass all stages, and mortality lipid mass all stages. Regional estimates Nansen Basin (NB), Fram Strait (FS), Greenland Sea (GS), W Spitzbergen Current (WSC), Iceland Sea (IS), E Norwegian Sea (ENS), W Norwegian Sea, (WNS) and Station M in the Norwegian Sea (NS). The twin bars in both panels indicate estimates for zero mortality (other than spent females the left bar), and a low mortality rate of 0.001 d^{-1} (the right bar) for all stages. The two panels depict flux estimated for different metabolic rates parameter *b*. Panel (**a**) $b = 2.5 \times 10^{-7}$ μgC$^{1/4}$ s^{-1} and (**b**) $b = 5.0 \times 10^{-7}$ μgC$^{1/4}$.

depth to which observations have to be made. In all likelihood, our abundances are underestimates, as over-wintering populations are probably deeper than most sampling depths. Much of our distribution knowledge of this species comes from spring and summer campaigns, often conducted on the shelf or in relatively shallow fjords and often only covering the upper 200 m of the water column. In addition to

abundance, a poorly constrained variable with large impact is the mortality rate of overwintering animals. We present two examples, one with no mortality (apart from spent females) and the other with very low mortality of 0.001 d^{-1} corresponding to a survivorship of 80% over the overwintering duration (Fig. 3). Mortality rates could easily be greater than this, and even a moderate increase to 0.005 d^{-1} would

bring about sequestration fluxes in excess of 10 gC m^{-2} yr^{-1}. Additionally, we present the outcome with different metabolic rate constants of 2.5×10^{-7} and 5×10^{-7} μgC$^{1/4}$ s^{-1} (panel a and b in Fig. 3). The consequence of higher metabolic rate is in moderate increase in the total flux. While respiration rate doubles, the length of diapause shortens from 8 months to less than 7 months for females, and from 7 to 3 months for stage CIII. A second consequence of higher metabolic rate is that females will be completely depleted after spawning. All of these considerations lend considerable uncertainty to our estimates although we do stress that in all cases we have tried to err on the side of caution. The three principal factors affecting this uncertainty in flux estimates, namely abundance, mortality and metabolic rate, are illustrated in Fig. 3. Further, the spreadsheet supplied in Supporting Information material will allow readers to judge for themselves the sensitivity of our estimates to particular parameter settings.

While the motivation for this work is partly to document how *C. hyperboreus* contributes to oceanic carbon sequestration, we feel it also important to address this in a more general sense. There are several copepod species in various regions of the global ocean that adopt similar life history strategies, and that locally, play key ecological roles. Specifically, there is a tight evolutionary coupling between zooplankton overwintering, the type and abundance of lipid available from their diet, the biochemical pathways by which dietary lipids are repackaged and stored, and the physical conditions found in their overwintering habitats. In this, lipids serve a triple purpose. They fuel metabolic costs during diapause (Hirche 1996; Lee et al. 2006), provide for capital breeding at an opportune time (Varpe et al. 2009; Sainmont et al. 2014), and provide a physical means for overwintering animals to achieve neutral buoyancy at depth (Visser and Jónasdóttir 1999; Pond and Tarling 2011). In part, it is the multipurpose use of lipids that makes these copepod species so successful, to the extent that they generally contribute a significant fraction of the local consumer biomass (Heinrich 1962), exerting significant predation pressure on the phytoplankton crop and their microzooplankton grazers while in turn being exploited as resources by forage fish.

In this sense, the significance of the lipid pump can be gauged in terms of the success of lipid-fuelled overwintering in the deep oceans as a life history strategy. We can speculate as to how global change might affect this success. In the first instance, there is the issue of changing phytoplankton community (Richardson and Schoeman 2004) and how this can affect not only the amount but type of lipid available to copepods. There is also the question of changes in deep water habitats as the pace and/or location of deep water formation changes (Rahmstorf et al. 2015). Increasing deep water temperatures not only increase respiration rates and thus decrease diapause durations, but also compromise ability of overwintering individuals to remain neutrally buoyant in these deep water habitats.

It is clear from this work, as well as previous studies, that the sequestration by overwintering zooplankton, while global in extent is far from uniform. There appear to be significant variations in intensity on the scale of 100s of km, with local hot spots and other regions with diminishing contributions. A landmark paper (Longhurst and Williams 1992) concluded that the carbon sequestered by seasonally migrating zooplankton was a minor contributor to the biological pump. This conclusion, drawn from a site in the North Atlantic, just happened to be in a location where practitioners of this life history strategy were scarce; likely due to the deep winter convection in this particular region that makes deep diapause less effective than in other areas. It was not until a more expansive mapping of overwintering populations was conducted (Heath et al. 2000) that a more complete regional estimate could be made (Jónasdóttir et al. 2015).

By way of conclusion, there is growing evidence of overwintering zooplankton populations in polar, subpolar, and temperate parts of the global oceans making significant contributions to oceanic carbon sequestration. The full extent remains unquantified as there are no easily obtained synoptic observations that can serve as proxies. Metabolic theory can certainly be used to constrain certain aspects for data poor species, although the abundance and distribution of overwintering populations remains the greatest unknown.

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Conflict of Interest
None declared.