1 **Lipid content in overwintering *Calanus finmarchicus* across the Eastern Subpolar North Atlantic**

2 **Ocean**

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Abstract

The boreal copepod *Calanus finmarchicus* accumulates lipid reserves during summer feeding in surface ocean waters, which enable it to stay at depth and survive famine during overwintering. Respiration of lipids during prolonged overwintering at ocean depths (>1000 m in some areas) has been shown to result in a net sequestration of carbon into the deep ocean: the so called 'lipid pump'. Here we provide a comprehensive synthesis of the geographic and vertical variations in lipid content of over-wintering animals across the Subpolar Eastern North Atlantic and, on the basis of this, we revise the estimates of carbon sequestration. Wax ester (WE) content ranged from 40 to 190 µg ind^{-1} at >250 m depths, with highest concentrations in the coldest (<0°C) waters at 400-600 m depth at the slope east of Faroe Islands and east of Greenland, and lowest in the warmer (>4°C) Irminger and Rockall Basins. Our new analysis results in about 44% higher estimates of carbon sequestration at up to 11.5 gC m^{-2}.

Introduction

Diapause is a trait that many Calanoid copepod species have adapted as a strategy to ensure maximum survival during periods of food shortage. The ideal and essential place for diapause is out of reach from predators, below the deep convection layer (Krumhansl et al. 2018) and in waters with lowered temperatures; a habitat that allows the organisms to remain quiescent with reduced basal metabolism during diapause.

Wax ester (WE) accumulation before a descent to depth of the oceans for overwintering is an essential adaptation,as being lipid rich while remaining torpid requires lipids with the physical properties of wax esters (Visser and Jónasdóttir 1999; Pond et al. 2012). The depth of overwintering is likely to be a function of the trade-off between predation risk and the physiological limitation of diapause. An important part of this physiological limitation has to do with how much lipids the copepods have at the start of diapause, and how fast the wax esters are catabolised as a function of their metabolic rate (Maps et al 2014). In order to better understand lipid accumulation strategies we need to know more about copepod overwintering habitats and the physiological restraints they face in terms of different temperatures and duration of diapause.

Calanus finmarchicus is a copepod species with a wide distribution in the subpolar North Atlantic spanning from Georges Bank in the west to Norway in the East, (Conover 1988; Heath et al. 2000). It accumulates wax esters as a pre adult stage C3-C5 before overwintering usually as stage C5 in deep ocean basins for a period that lasts from 120 to >300 days (Hirche 1996; Maps et al. 2014; Melle et al. 2014; Jónasdóttir et al. 2015; Wilson et al. 2016). The winter distribution of *C. finmarchicus* is probably the best known of all copepod species (Heath et al. 2004). The winter population reaches densities of 35-

56,000 indiv. m^{-2} in the Eastern and central Norwegian Sea (Dale et al. 1999; Heath et al. 2004) and
Lofoten Basin (Halvorsen et al. 2003) with pockets of high densities of 15-60,000 indiv. m^{-2} in the Nova
Scotia and Newfoundland basins (Head and Pepin 2007), Gulf of Maine (Runge et al. 2015) and Iceland
Sea (Gislason and Silva 2012). Overwintering populations are also found in high densities in fjords and
estuaries on both sides of the Atlantic (e.g. Plourde et al. 2001; Arnkværn et al 2005; Clark et al. 2012).
The overwintering parking depth varies in the different North Atlantic Basins and is most often found to
be below the lower boundary of the cold intermediate layer (Heath et al. 2004; Krumhansl et al, 2018).

Lipid accumulation prior to diapause by the pre-adult copepodite stage 5 (C5) is well documented
(Køgeler et al. 1987; Falk-Petersen et al. 1987; Kattner and Krause 1989; Miller et al. 1998; Jónasdóttir
1999). The lipid of late-stage C5 *C. finmarchicus* typically exceeds 50% of its dry weight (Kattner and
Hagen 2009), with up to 90% of total lipids being wax esters (Lee et al. 2006). While diapause depth of
C. finmarchicus varies, they usually are found at depth of 500 to 1500 m during winter in water
temperatures of -0.5 to 5 °C (Heath et al. 2004). Overwintering at shallower depths and at higher
temperatures has however, been observed in coastal fjords (e.g. Clark et al. 2012, Bagøien et al 2001).
Duration of diapause is likely to be greatly influenced by storage lipid fullness, overwintering
temperatures and geographical location, but increased respiration due to higher metabolism with
increasing temperatures is likely the main factor affecting duration of diapause (Wilson et al. 2016).

Lipid metabolism by copepods in diapause has recently been shown to be a substantial contributor to the
North Atlantic biological carbon pump (Jónasdóttir et al. 2015; Visser et al. 2017). Respiration by the
overwintering population of *Calanus finmarchicus* alone has been shown to equal the passive carbon
sequestration flux in the North Atlantic and has been named "the lipid pump" (Jónasdóttir et al. 2015).

83 Along with accurate measures of abundance, a reliable estimate of diapause duration is crucial for

84 assessing the lipid driven carbon sequestration. To date, to our knowledge, only two studies (Johnson et

85 al. 2008; Melle et al. 2014) have estimated diapause duration of populations using field observations,

86 based on percentages of C5 and adults in relation to the historical population structure in autumn and

87 spring at given locations. Diapause duration has on the other hand been modelled by Ingvarsdóttir et. al

88 (1999), Saumweber and Durbin (2006), Johnson et al. (2008), Maps et al. 2011 and Wilson et al. (2016).

89 These studies and models show a broad range of durations ranging from 70 to well-over 300 days,

90 depending on location.

91

92 Here we present results of the mapping of the lipid content of over-wintering *C. finmarchicus* in 7 basins

93 and one shelf-sea in the Subpolar Eastern North Atlantic. The measures were conducted on a series of

94 late autumn/winter cruises and present the most detailed geographical and vertical coverage of lipid

95 content of this species during diapause to date. We use the observed horizontal and vertical distribution

96 to estimate respiration and diapause duration of the different populations by applying a model presented

97 by Visser et al. (2017), which is based on metabolic theory and isomorphism. This model is then used to

98 re-estimate the carbon sink due to over-wintering *C. finmarchicus* respiration and mortality by applying

99 the new measure of diapause duration, including respiration rate estimates of the C4 and C6 females

100 observed in the overwintering populations, and adding carbon loss by mortality during the overwintering

101 period.

102

103 **Methods:**

104 Lipid content data were derived from two sources: our own chemical analyses, and previously published

105 studies. *Calanus finmarchicus* for our own analysis were collected for lipid analysis during 14 winter

106 field campaigns on RVs DANA (DTU Aqua, Denmark), Scotia (Marine Scotland Science, UK), and

107 Bjarni Sæmundson (Marine Research Institute, Iceland). The sampling covered the periods from

108 September to February from 1993 to 2012 in 8 different areas of the Subpolar Eastern North Atlantic.

109 The stations sampled can be allocated to the following ocean areas: Irminger Basin (IRM), East

110 Greenland (EGR), Iceland Sea (ICS), Iceland Basin (ICB), Rockall Basin (ROC), Western Norwegian

111 Sea (WNS), Eastern Norwegian Sea (ENS) and the North Sea (NS) (Figure 1; Table 1). The southern

112 EGR stations would in principle be a part of ICS while the northern stations are in the Greenland Sea but

113 are here grouped as EGR as the copepods are sampled in the East Greenland Current at the same time of

114 year, while the ICS copepods are sampled further east in the Iceland Sea Gyre and East Iceland Current.

115

116 During the Dana and Scotia cruises in 1993-2002, copepods were collected with the ARIES multinet

117 system (Dunn et al. 1993) that collected samples at approximately 50 m intervals to a depth of

118 approximately 3000 m. In some instances, ring nets (250 μm mesh, 1 m diameter mouth aperture) with a

119 5 L non-draining cod-end were used to sample the upper 200 m stratum. On Bjarni Sæmundsson and the

120 2012 Dana cruise, samples were taken with multinets in 7-10 depth layers covering the whole water

121 column and ring nets. The ARIES was equipped with a Seabird CTD while CTD profiles were taken at

122 all stations where multinets and ring nets were deployed. As soon as possible after retrieval of the nets,

123 *C. finmarchicus* stages C5 and female C6s were sorted under a stereo microscope. Up to 10 intact, and

124 preferably live, individuals were placed in cryovials, the air in the vials replaced with nitrogen gas and

125 the samples frozen immediately in liquid nitrogen. Samples were kept on ice at all times prior to and

126 during sorting. At the end of the cruise, the samples were transferred to a -80°C freezer for storage until

127 analysis.

128

129   Prosome length (PL) of animals was measured to the nearest 0.01mm. Length measurements of

130   *Calanus finmarchicus* from a Faroe Shetland Channel transect (Dana cruises in 1993-1995) area and

131   Irminger Sea have been presented as grouped averages in Jónasdóttir (1999) and Heath et al. (2008),

132   respectively. All lipid analysis was carried out using Iatroscan TLC as described in Jónasdóttir (1999).

133   Lipid content was standardised to prosome volume (PV) in mm^3 according to Miller et al. (2000): PV=

134    $0.0292 \times PL^{3.6699}$ where PL is the average prosome length in mm for the copepodite stage at the

135   corresponding sample location and depth. Size measurements and lipid analyses were not performed on

136   the same individuals.

137

138   *Oil sac area*. Copepods from the Greenland Sea were photographed, after which the area of the lipid sac

139   was traced using the "image-J" software (Rasband , 1997– 2009). The pixel-to-mm ratio was calibrated

140   using the image of the appropriate calibration slide. The lipid sac area was converted into wax esters by

141   using the formula $\mu g \, (WE) = 0.167 \times A^{1.42}$ from Vogedes et al. (2010) where A is the area of the lipid

142   sac in mm^2.

143

144   *C. finmarchiucs* dry mass was measured from most sampling locations. Individual copepods were

145   measured for prosome length, dried in batches of 3-10 individuals at 60°C and weighed on a Cahn 26

146   Automatic Electrobalance. The dry mass (DW) therefore includes lipids. In other instances dry mass was

147   estimated from prosome length (PL) using the length/DW equation: $DW = 0.0106 \times PL^{3.64}$, where DW

148   is in mg and PL in mm based on the relationship of copepods from winter in the Norwegian Sea

149   (Ingvarsdóttir et al. 1999). Carbon mass was estimated using the equation: $C = 0.623 \times DW - 0.0143$

150   from Ingvarsdóttir et al. (1999).

151

Previously published data

153   Additional lipid data used in the analyses were compiled from our own previously published studies

154   shown in Table 1 and locations of the samples included in Fig. 1. The original data from the Irminger

155   Sea (Discovery 258 and 267) published as % C in Heath et al. (2008), are here re-presented on an

156   individual and volume basis to be comparable with the present data.

157

158   *Estimate of diapause duration*

159   Respiration of copepods in diapause was calculated based on metabolic theory and the isomorphism

160   model presented in Visser et al. (2017):

161
$$r\,(M,\,T) = b \times M^{3/4} \exp\left(E \times (T\text{-}T_0) \,/\, (k \times T \times T_0)\right) \quad \text{(Eq. 1)}$$

162   where M [μgC] is mass, r [μgC s^{-1}] is respiration rate, T [K] is temperature in Kelvin, b [μgC$^{1/4}$ s^{-1}] is a

163   universal scaling constant, E[eV] is the activation energy and k [eV K^{-1}] the Boltzmann constant. T_0 is

164   base temperature, taken to be T_0= -273 °C (absolute zero). We used universal scaling constant b of 2.5 ×

165   10^{-7} μgC$^{1/4}$ s^{-1} as suggested by Visser et al. (2017).

166

167   The model is carbon based and includes estimates of structural mass m that scales with prosome length

168   (PL) as: m=αPL^3. Maximum wax ester content is expressed as $w_{max} = \beta$PL^3, and minimum wax ester

169   content $w_{min} = \delta\beta$PL^3. The coefficients α and β are determined by a best fit regression of maximum total

170   carbon content (α) (from dry weight) and maximum carbon based WE content (β) per prosome length

171   observed for different sized copepods from stages C4 to C6F from the present study. WE was converted

172   to carbon by assuming that 79% of its weight is carbon, calculated from WE fatty acid and alcohol

173   profiles of Arctic *C. finmarchicus* summarized in Kattner and Hagen (2009). Diapause duration was

174   estimated as the time it would take to respire the lipid to at least 20%. Therefore, minimum wax ester

175   content is 20% ($\delta = 0.2$) of the maximum capacity as suggested by Saumweber and Durbin (2006). We

176   refer to the supplementary information in Visser et al. (2017) for full details of the model equations.

177

178   *Estimate of carbon sequestration*

179   The two factors that contribute to carbon sequestration during the period of overwintering are respiration

180   and mortality. The estimated respiration rates were used to calculate the carbon sink overwintering

181   copepods leave behind as respired CO_2 to compare with the previous estimates of the *C. finmarchicus*

182   lipid pump (Jónasdóttir et al. 2015). The present estimate includes additional sequestration by stage C4

183   and C6 females, as well as a modest mortality not considered in the previous published lipid pump

184   estimate.

185

186   Overwintering copepods face mortality due to predation, starvation and other causes. Only a few

187   mortality rate estimates of overwintering *C. finmarchicus* are available, but they range from 0.004 d^{-1} for

188   the Iceland Basin and the Irminger Sea (Gislason et al. 2007) and 0.007 d^{-1} for the Norwegian Sea

189   (Bagøien et al. 2001). It is uncertain which fraction of these mortality estimates are due to predation, or

190   non-predatory mortality or the estimate is not a mortality but advection loss. We here use a conservative

191   estimate of 0.001 d^{-1} as non-predatory mortality that directly adds both structural and lipid bound carbon

192   to the carbon flux on the cost of respired carbon. This non-predatory mortality is likely to differ

193   between habitats but in lack of better knowledge we keep it constant in our calculations.

194

195   *Statistics*:

196   Differences between depths and areas were tested with one way ANOVA and if not normally distributed

197   with Kruskal-Wallis ANOVA on ranks. When significant differences were observed, a pairwise post-

198   hoc Dunn's and Holm-Sidak tests were conducted on nonparametric and parametric data, respectively.

199   Multiple regression was run on log transformed WE data due to non-normal distribution in relation to

200   month, depth, temperature and size.

201

202   **Results:**

203   *Prosome length*

204   The size of the overwintering C5s *C. finmarchicus* differed between the geographic areas (One way

205   ANOVA on ranks, $H = 179.55$; $df = 7$; $p < 0.001$; Fig. 2a). In general, size did not differ between the

206   depth layers within an area with the exception being the individuals at the surface and at 500-1000m

207   depth in the Eastern Norwegian Sea and the two depth layers in the North Sea, surface individuals being

208   smaller in both areas. Detailed statistics of the comparison within areas is shown in Supplementary

209   Table 1. Two main size groups were observed, the larger C5s off East Greenland and the Iceland Sea

210   (2.47 ± 0.02 and 2.43 ± 0.03 mm $\pm SE$; n=98 and 15 respectively) and smaller individuals in the Irminger

211   Sea and the North Sea (2.16 ± 0.02 and 2.22 ± 0.02 mm, $n = 39$ and 37 respectively). In the other basins

212   the C5s measured between 2.3 and 2.4 mm and did not statistically differ from the smaller and larger

213   groups. In Fig. 2a we additionally plot published sizes of *C. finmarchicus* C5 from the Labrador Sea

214   (Pepin and Head 2009) which are comparable with the larger group in off East Greenland and Iceland

215   Sea. Non-significant differences of the basin means are shown in Fig. 2a with the same lower letters

216   over the bars based on Holm-Sidak all pairwise comparisons.

217

218   *Lipid content*

219   Most *C. finmarchicus* collected were at stage C5. Individual lipid content of stage C5 differed between

220   the basins (Fig. 2b), and were highest off East Greenland where the average wax ester (WE) content per

221   individual measured 155 ± 7 µg ind^{-1} ($\pm$ *SE*). The lowest content was observed in the Irminger Sea,

222   Iceland Basin and the North Sea (51 ± 7, 51 ± 4 and 44 ± 6 µg WE ind^{-1} $\pm$ *SE*). As lipid storage capacity

223   is a function of size (Fig. 3) the WE content was standardized to prosome volume (Fig. 2c). The

224   copepods in the Greenland Sea had the highest standardized value while the copepods in the Irminger

225   Sea had the lowest lipid content per prosome volume. The differences in standardized lipid content were

226   not significant between most of the basins with the exception of the Greenland Sea copepods. However,

227   the standardized lipid content in the Western Norwegian Sea and Iceland Sea were not significantly

228   different from the East Greenland copepods (Holm-Sidak all pairwise multiple comparison).

229

230   The average triacylglycerol (TAG) content in the copepods was generally low ranging from 0.1 to 4.8

231   µg ind^{-1} (Table 2), with statistical difference between the basins ($H = 153.174$; *df* $= 6$; $p < 0.001$).

232   Posthoc Dunn's Method on all pairwise comparison showed that the difference were due to statistically

233   higher TAG content ($p < 0.05$) in copepods from the Norwegian Sea (East and West) and North Sea

234   compared to the Irminger Sea, Iceland Sea, Iceland Basin and Rockall Basin. TAG was not measured in

235   copepods off East Greenland.

236

237   Total lipids in C5s ranged from being 27-56% of dry weight, except for Irminger Sea (6.2-7.8%), and

238   wax esters from 54-92% of total lipids (Figure 4, Table 2). The general trend in lipid accumulation was

239   over 50% of the total dry mass off East Greenland, the Iceland Sea and Norwegian Sea (East and West)

240   but between 30 and 40% in Rockall and the Iceland Basins and the North Sea. In most areas 80% of the

241   total lipids were composed of WE with the exception of the North Sea where the WE composition was

242   54%.

243

244   There were 2 distinctive temperature systems in the 7 basins; the areas where the deep water was at

245   about 0°C (EGR, ICS, WNS and ENS) and the areas where the water was >4°C (IRM, ICB, ROC) (Fig.

246   5a). Standardized wax ester content was generally higher in copepods residing in colder deep water mass

247   (white bars in Fig. 5b). This difference was statistically significant at most depths, with the exception at

248   the average 875 m depth (statistics shown in the figure and in supplementary Table 2A). The wax ester

249   content was also higher in the cold water group when binned at their ambient temperature, with

250   significant differences at temperatures from 2-8 °C (see statistics in the figure and in supplementary

251   Table 2A), but the difference between the groups was not significant in ambient waters of >8 °C

252   reflecting the surface waters in the cold water group (Fig. 5c).

253

254   The most frequent sampling of *C. finmarchicus* lipid content was from the Faroe Shetland Channel. The

255   winter WE content in stage C5 *C. finmarchicus* at >600 m depth differed statistically between years

256   from 1997-2003 (One Way ANOVA: $F_7 = 4.8$, $p < 0.001$) where the WE content during 99-00 was

257   higher than in 93-94, 94-95 and 95-96 (Holm-Sidak Pairwise Multiple comparison t = 3.9, 3.8 and 3.8

258   and P= 0.004, 0.005 and 0.005 respectively) (Fig. 6A). When standardized to size the difference in WE

259   content (WE/Vol Fig 6B) in 99-00 was higher than 94-95 (Kruskal-Wallis One Way ANOVA on ranks

260   H_6=16.14, P=0.013, Pairwise Multiple comparison Q=3.43, P=0.13). Combining monthly measures

261   from all sampling years a difference was observed for WE content (Kruskal-Wallis One Way ANOVA

262   on ranks H_5=16.84, P=0.005) (Fig. 6C) while Dunn´s post-hoc test could not isolate the groups that

263   caused that difference (all pairs with P> 0.08). No measurable statistical difference could be observed

264   in standardized WE content (WE/Vol) between the months.

265

266   *Diapause duration and carbon sequestration*

267 The carbon vital mass (C_{max}) and maximum wax ester content (w_{max} as carbon) as a function of prosome

268 length are shown in Figure 7, where $\alpha = 19$ and $\beta = 14$. Therefore, the maximum WE carbon content that

269 best fitted the data, $w_{max} = 14\ PL^3$ and the structural mass, $C_{max} = 19\ PL^3$. The minimum WE carbon

270 content w_{min} is presented as 20% of the w_{max}.

271

272 Stage based individual respiration rates varied 3 fold from 0.65 (C4 in ENS) to 2.30 µgC d^{-1} (Female in

273 LS) dependent on size and temperature (Table 3). This is similar to the reported values for dormant *C.*

274 *finmarchicus* at 0°C from the Faroe Shetland Channel in December and January of 0.1 to 0.7 µgC d^{-1}

275 (Ingvarsdóttir et al. 1999) and 0.4-0.9 µgC d^{-1} at 6°C (Hirche 1983). Maximum estimated overwintering

276 period for C5 *C. finmarchicus,* assuming minimum WE reserve level of 20%, was shortest in the

277 Rockall Basin and North Sea (89 and 81 days respectively), Iceland Basin (119 days), and longest in the

278 Iceland Sea (204 days).

279

280 Integrating the respiration rate over diapause duration and stage abundance gives the respired carbon

281 ranging from 0.4 to 8.8 gC m^{-2} (Fig.8). This value was highest in the Eastern Norwegian Sea due to high

282 copepod abundance and long diapause duration (187 days for C5). Estimated mortality added about 12-

283 25% to the respired carbon flux as combined structural and lipid bound carbon resulting values as high

284 as 11.5 gC m^{-2}.

285

286 **Discussion:**

287 The present study comprises the most extensive geographic, horizontal and vertical coverage of *Calanus*

288 *finmarchicus* winter-lipid content to date. It represents a collage of a 6 month overwintering period

289 (September to February) spanning over 8 different years. Our data synthesis has revealed a clear and

13

290 unique picture of the different thermal habitats of this species in the Subpolar North Atlantic basins and

291 offers a valuable resolution of overwintering copepods for further modelling of diapause duration (*cf.*

292 Pierson et al 2013).   Admittedly, the study does not cover all overwintering areas of this species, with

293 notable exception being the populations in the deeper waters off Newfoundland and the Scotian Shelf.

294 As open-ocean winter sampling is treacherous and haphazard due to bad weather conditions, only a few

295 earlier winter data were available that we could use for our analysis in the present study.

296

297 The results have implication for our understanding of the role of advection in the population dynamics

298 of *C. finmarchicus* in the central Atlantic. The prosome lengths of the Irminger Sea C5 *C. finmarchicus*

299 in diapause were smaller (<2.2mm) than expected considering the observed C5 prosome length of 2.4-

300 3.0 mm in the upper 100 m in the Irminger Sea during late spring and summer (Yusuf and Webster

301 2008; Jónasdóttir personal observations). The overwintering sizes of the C5s correspond well to the ones

302 in the Iceland Basin, but not in the Iceland Sea and off the Greenland coast. Therefore, it is possible that

303 the Irminger Sea overwintering population may originate from the Iceland Basin, while the summer and

304 spring surface populations are advected along with the Greenland Coastal current from the Greenland

305 Sea. The low lipid content in copepods sampled deeper than 500 m in November and December in the

306 Irminger Sea and the Iceland Basin comprise less than 21% (ca 43 μgC indiv^{-1}) of the estimated

307 maximum WE content for that size (w_{max} = 192 μgC indiv^{-1}). Therefore, based on the assumption of the

308 model of 20% remaining for ascent, the copepods would not survive the overwintering period and will

309 probably not be able to make it to the surface in spring by lipid driven buoyancy assisted force. The lipid

310 reserve would last about 40 days with the estimated respiration rate of 1.26 μgC day^{-1} during diapause at

311 5 °C. Therefore, these individuals are probably lost from the spring recruitment except if they have

312 other assisted forces (such as upward mixing by the aid of the deep convection layer) to bring them to

313   the surface in spring or the copepods have even lower metabolic rates than we use in our model

314   predictions.

315

316   It is clear from the present observations that size matters. Comparing *C. finmarchicus* in the basins with

317   ~4°C overwintering habitats, the C5s in the Labrador Sea were larger than the C5s in the Irminger and

318   Iceland Basins. Being large is beneficial in warmer overwintering waters, having more lipid storage

319   capacity and relatively lower metabolic rates. Our calculations show that the Labrador Sea copepods can

320   survive a whole month longer overwintering periods (142 d) than those in the Irminger (121 d) and

321   Iceland Basin (119 d) copepods.

322

323   A month can make a huge difference for survival in spring. Large differences are observed in the

324   remaining lipid reserves of *C. finmarchicus* in spring between Eastern and Western Subpolar North

325   Atlantic basins. In the Norwegian Sea Basins and Iceland Sea to the East, the lipid reserves after ascent

326   are about 150 µg WE ind^{-1} for a C5 and 80-100 for a C6 female (Jónasdóttir 1999; Jónasdóttir et al.

327   2008) allowing gonad development to take place before the spring bloom (Niehoff et al. 1999) and

328   initiate some lipid based spawning (Richardson et al. 1999; Jónasdóttir et al. 2008). In the Labrador Sea

329   and Disko Bay, West Greenland final gonad maturation and hence spawning do not take place until after

330   the initiation of the spring bloom. In Disko Bay the females loose about 47% of their WE (from 75µg to

331   40 µg) before the spring bloom starts, but do not seem to direct their energy into development of gonads

332   or to produce eggs, indicating lipid catabolism is used for basic metabolism only (Niehoff et al. 2002;

333   Swalethorp et al. 2011). The bet-hedging strategy of pre-bloom spawning used by the populations on

334   the eastern side of the Atlantic appear not to be beneficial for the western populations. The timing of the

335   spring bloom is therefore critical for the Western Atlantic populations and may play an important role in

336   the success of populations with shorter overwintering periods.

337

338   Jónasdóttir et al. (2015) and Visser et al. (2017) showed the importance of copepod respiration during

339   overwintering for the overall carbon sequestrations of the oceans and named it the lipid pump. The lipid

340   pump estimates for *C. finmarchicus* in Jónasdóttir et al. (2015) were based on the model approach of

341   Saumweber and Durbin (2006) using their respiration rates but otherwise the same *C. finmarchicus* data

342   presented here (compared in Fig. 8). However, Jónasdóttir et al. (2015) did not include any mortality in

343   the estimates of carbon sequestration and included only stage C5. Here, we use the most recent method

344   presented in Visser et al. (2017) based on metabolic theory as presented in Maps et al. (2014) which

345   results in higher estimates of the lipid pump than in Jónasdóttir et al. (2105). The Saumweber's approach

346   used in Jónasdóttir is nonlinear while Visser's approach is linear.

347

348   Diapause duration is a crucial factor in life history of overwintering copepods (Dahms 1995, Pierson et

349   al. 2013). While it is challenging to estimate from field observations the modelled durations used in our

350   lipid pump estimates are consistent with those few observations that do exist. Our model resulted in

351   diapause durations between 90 and 205 days which is slightly shorter but comparable to the field based

352   estimates of Melle et al. (2014) and in good agreement with the model estimates of Maps et al. (2014)

353   while falling mid-way between the estimates of Saumweber and Durbin (2006) and Johnson et al.

354   (2008). Our carbon sequestration estimates are on average 44% higher than presented Jónasdóttir et al.

355   (2015) due to longer diapause duration, mortality (structural and lipid mass carbon) and higher

356   population abundance due to inclucion of C4s and females. The two models show calculations within

357   the same order of magnitude in the respired based carbon, with the largest difference between the

358   models in the coldest water masses (ICS, WNS and ENS). Respiration is the largest contributor to

359   carbon sequestration by diapausing *C. finmarchicus*, but even low mortality rate add 10-30% to the

360   estimates of respired carbon.

361

362   The calculations of the lipid pump and the potential diapause duration face two significant uncertainties

363   that can potentially be resolved by future research: overwintering respiration rates and the relationship

364   between prosome length and lipid levels. Indeed, *C. finmarchicus* appears to have particularly low

365   metabolic rates (Maps et al 2014) and fast development rates (Banas and Campbell 2016) compared to

366   other copepod species. Lowering of the metabolic rates to even lower as shown for *C. finmarchicus*

367   sized copepods in Maps et al (2014) would result in lower respiration rates, but in turn also slower lipid

368   catabolism allowing longer duration of diapause. Relationships between body size, temperature and

369   overwintering respiration rates have now been established for a number of copepod species (Maps et al.,

370   2014) but a large amount of uncertainty remains about the precise relationships and whether they are

371   geographically consistent. Furthermore, it is unclear and possibly impossible to establish if the

372   respiration rates, which are estimated using diapausers brought to the surface, are truly reflective of

373   those in deep waters of up to 1000 m.

374

375   Similarly, the relationship between prosome length and maximum wax ester levels in ours and other

376   studies are variable and potentially imply that there is significant geographic range in this relationship.

377   For example, the relationships in Miller et al. (2000) and Saumweber and Durbin (2006) give much

378   higher storage lipid estimates than observed in other studies while that of by Pepin and Head (2009) fits

379   our data very well. The model of diapause duration reported here therefore differs from those of Wilson

380   et al. (2016) and Saumweber and Durbin (2006) due to being derived from different prosome length-wax

381 ester data sets. Future work should therefore establish if this geographic variation in the relationship

382 between prosome length and lipids is due to regional adaptations to differing overwintering habitats or

383 to variation in growth conditions before diapause.

384

385 *C. finmarchicus* being a key species in the North Atlantic food web makes prediction of the fate of the

386 species with warming of the North Atlantic crucial. While warming of the deep overwintering habitats

387 are not seen as an imminent threat in the deep ocean basins, the warming of the surface waters is

388 predicted to increase more rapidly in the Arctic and Subarctic regions compared to other oceanic regions

389 (IPCC 2014). *C. finmarchicus* populations appear to be moving further north with the warmer currents

390 (e.g. Chust et al. 2014) with implications for export of carbon flux across the whole North Atlantic Basin

391 (Brun et al. 2019). However, while overwintering habitats may stay stable and within the tolerable range

392 for successful overwintering, the warmer surface waters will inevitably result in faster growth and

393 smaller sized copepods (Campbell et al. 2001, Forster and Hirst, 2012). Maps et al. (2014) cautioned

394 against using surface conditions during growing seasons only for estimating climate impacts on

395 diapausing copepods. However, warming of the surface waters will affect overwintering indirectly by

396 reduced lipid storage capacity that may in turn affect the maximum duration of diapause (Pierson et al.

397 2013), similar to what the present study shows to be the case in the Irminger Sea and Iceland Basin. The

398 importance of warmer surface water for overwintering is therefore more related to the reduced lipid

399 storage capacity that may in turn affect the maximum duration of diapause has currently an unforeseen

400 consequence for this key species across the Northern North Atlantic ecosystem.

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548

550 **Figure 1.** Sampling locations for lipid content of *C. finmarchicus* during winter. The dotted lined boxes

551 surround the different ocean basins IRM: Irminger Sea, EGR: East Greenland, ICS: Iceland Sea, ICB:

552 Iceland Basin, ROC: Rockall Basin, WNS: Western Norwegian Sea, ENS: Eastern Norwegian Sea, NS:

553 North Sea. LS: Labrador Sea from which literature data were obtained.

554

555 **Figure 2.** *Calanus finmarchicus*, average $\pm$ *SE* of a) prosome length (mm) b) wax ester content (μg

556 individual^{-1}) and c) Wax ester per unit prosome volume (μg mm^{-3}) in 4 different depth layers across the

557 Subpolar North Atlantic basin (from light grey to black, 0-250, 250-500, 500-1000m and >1000m depth

558 layers). The same lower case letters above the clusters of bars indicate no significant difference between

559 the basins as tested by Dunnet's post hoc pairwise comparison. LS: size from Pepin and Head (2009).

560 Ocean Basin abbreviations as in Figure 1.

561

562 **Figure 3.** Wax ester content (μg individual^{-1}) of *C. finmarchicus* as a function of prosome length (mm).

563 Current study: black dots. Comparison to other studies open diamonds: Miller et al. (2000) their

564 equation: oil sac volume OSV $= 0.5822$ PL $- 1.0208$ adjusted to μg WE; open circles: Pepin and Head

565 (2009) only showing their maximum measures of the lateral oil sac area adjusted to WE using the

566 equation of Vogedes et al. (2010); open downwards triangles: Bergvik et al. (2012) transposing oil sac

567 volume to WE by using 900μg/mm^{3} as suggested by Miller et al. (1998); and open upwards triangles:

568 Vogedes et al. (2010 in supplementary information).

569

570 **Figure 4**. *C. finmarchicus* total lipid (TL) and wax ester (WE) content as % fraction of dry weight (DW)

571 $\pm$ *SE*, in the different North Atlantic Basins. Abbreviations same as in Table 1. The WE fraction of total

572 lipids is listed at the end of the bars. For EGR the WE proportion is assumed to be the same as in the

573 ICS.

574

575 **Figure 5.** A) Temperature and depth for the samples collected and analysed for lipids from all cruises.

576 B) Mean (dotted line), median (solid line) and 5th and 95th percentile of WE/Vol (μg mm^{-3}) in C5 *C.*

577 *finmarchicus* at different B) depth layers and C) temperature ranges. Open symbols and white boxes:

578 sampling in EGR, ICS, WNS and ENS; grey symbols and boxes: sampling in IRM, ICB, ROC and NS.

579 Results from One-Way ANOVA on Ranks: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

580

581 **Figure 6.** Average (dotted line), median (solid line) and 5th and 95th percentile of WE (μg ind^{-1}) content

582 and WE/Vol (μg mm^{-3}) in stage C5 *C. finmarchicus* from >600 m depth in the Faro Shetland Channel

583 during A) and B) 8 winters (September to March); C and D) 6 winter months all years averaged. *n*:

584 number of samples behind in the analyses, the same lower case letters above the bars in A and B indicate

585 a statistical difference.

586

587 **Figure 7.** Wax ester content (ω [μgC]) as function of prosome length (PL [mm]) across stages C5 for *C.*

588 *finmarchicus*. Solid dots are the maximum WE content as carbon per unit length from the present study.

589 Power law regressions to the observations (black dotted line, excluding the largest individuals with

590 relatively low lipids) suggest $\omega[\mu gC] = 2.18\ PL^{4.79}$ ($R^2 = 0.82$). Superimposed (black solid lines) are

591 estimates of the maximum and minimum carbon based wax ester content $\omega_{max} = \beta\ PL^3$ and $\omega_{min} = \delta\beta$

592 PL^3 respectively, and carbon based vital (structural) mass $C_{max} = \alpha\ PL^3$ based on isometric scaling (se

593 methods for details). Carbon mass regressions in light grey dotted lines are results from Ingvarsdóttir et

594 al. (1999), Madsen et al. (2001) and Swalethorp et al. (2011).

595

596   **Figure 8**. Regional estimates of the carbon flux associated with overwintering populations of *C.*

597   *finmarchicus*. Estimates are broken down as to respired flux (grey fill), mortality structural mass all

598   stages (green fill) and mortality lipid mass all stages (dark grey fill). Regional estimates Labrador Sea

599   (LS), Irminger Sea (IRM), East Greenland (EGR), Iceland Sea (ICS), Iceland Basin (ICB), Rockall

600   Basin (ROC), E Norwegian Sea (ENS), W Norwegian Sea (WNS) and North Sea (NS). White line

601   indicates contribution of stage C5 to the flux. Parallel shaded column is the results from Jónasdóttir et

602   al. (2015) based on C5 flux only without mortality.