

1 **Photoperiodism and overwintering in boreal and sub-Arctic** 2 ***Calanus finmarchicus* populations**

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21 Locomotor Activity, Latitudinal, Seasonality, Lipid, Overwintering, Zooplankton.

22
23 **Short title: *Calanus finmarchicus* overwintering**

24
25 The copepod *Calanus finmarchicus*, a key species in the North Atlantic, generally spends the
26 non-productive season by descending into deep waters and entering diapause, a physiological
27 state characterized by reduced metabolism and arrested development. In the open ocean,
28 overwintering depths are below 600 m where temperature and light conditions are favourable
29 to initiate diapause. However, *C. finmarchicus* has also been reported diapausing in areas with
30 shallow water depth such as fjords, coastal waters and shelf seas. In these environments, the
31 temperature and light conditions are different, and it has been hypothesized that under such

32 conditions *C. finmarchicus* may remain active throughout winter. Here, we investigated
33 changes in the swimming activity of *C. finmarchicus* from shallow fjords in the eastern North
34 Atlantic during overwintering in response to ambient photoperiod. We conducted monthly
35 experiments with populations from two fjords from different latitudes (sub-Arctic Ramfjord,
36 69°N and boreal Loch Etive, 56°N), measuring the locomotor activity of individual *C.*
37 *finmarchicus* CVs exposed to a natural light: dark cycle. At both locations, peaks in activity in
38 response to the light cycle were observed to shift from nocturnal during the early overwintering
39 phase to diurnal during mid and late overwintering phase, with a minimal intensity observed
40 during the mid-overwintering phase. In Ramfjord, activity and rhythmicity were generally
41 lower than in Loch Etive. We conclude that *C. finmarchicus* remains active throughout its
42 overwintering period when in shallow (< 200 m) locations but down-regulates its locomotor
43 activity during the main overwintering phase, which we describe as a winter resting state as
44 distinct from classical diapause.

45 **1 Introduction**

46 The primarily herbivorous copepod *Calanus finmarchicus* is a key species in the North
47 Atlantic marine ecosystem. It plays a major role in the transfer of energy from phytoplankton
48 to higher trophic levels due to its ability to accumulate large amounts of lipids (Falk-Petersen
49 et al. 2009). *Calanus finmarchicus* also contributes to the biogeochemical carbon cycle by
50 releasing organic matter at depth through its diel and seasonal vertical migration (SVM). The
51 lipid storage and SVM behaviour not only confer *C. finmarchicus* an essential role in the
52 ecosystem, but ensure survival through the non-productive period, i.e., when food availability
53 is reduced, and thus ultimately improve reproductive success (Maps et al. 2011). SVM is
54 observed in a number of pelagic organisms and describes the seasonal migration from the upper
55 pelagic to deeper waters at the end of the productive season, and an ascent to surface layers in
56 late winter/ early spring. When at depth, *C. finmarchicus* enters a physiological state, called

57 diapause (hereafter referred to as classical diapause), characterized by reduced metabolism, as
58 well as reduced enzymatic, feeding and swimming activity (Marshall & Orr 1955, Hirche 1983,
59 Hirche 1996). During this time, development is arrested to a late developmental stage, which
60 in this species is most commonly the copepodite stage V (CV) (Marshall & Orr 1955, Hirche
61 1983, Hirche 1996). This overwintering strategy enables *C. finmarchicus* to reduce its
62 metabolic costs and risk of being preyed upon by visual predators during the non-productive
63 period, due to cooler temperatures and darkness of the deep-water environment (Marshall &
64 Orr 1955, Hirche 1996).

65 Diapause is a well-known behaviour in *C. finmarchicus*, but the initiation of diapause is
66 poorly understood. Several factors are commonly recognized as involved in the initiation of
67 diapause, including exogenous seasonal cues such as photoperiod, temperature, food
68 availability, predation pressure, and endogenous cues such as lipid thresholds and circadian
69 clocks (Irigoiien et al. 2004, Häfker et al. 2017). However, diapause initiation appears to be
70 more complex than a simple response to one of these factors. It has been suggested that a
71 combination of factors may trigger diapause and that these factors may change geographically.
72 Baumgartner & Tarrant (2017) suggested that cues may differ between animals inhabiting
73 environments with shallow water depth and those inhabiting environments with deep water
74 depth and polar environments. They contend that in locations with shallow water depth,
75 diapause is triggered by a combination of factors such as photoperiod (Sømme 1934, Fiksen
76 2000), temperature (Corkett & McLaren 1979), food abundance (Rey-Rassat et al. 2002) or
77 predation pressure (Ji 2011), while for organisms living in the deep oceanic basins and in polar
78 environments a single seasonal cue such as photoperiod or temperature may be enough to
79 induce diapause. For the latter, organisms inhabiting environments with shallow depth at high
80 latitudes should respond similarly to those from deep environments.

81 The distribution of *C. finmarchicus* extends from 40° N to 80° N (Hirche & Kosobokova
82 2007, Choquet et al. 2017, Grieve et al. 2017). Along this distributional range, it is exposed to
83 a large gradient of environmental conditions including seasonal changes in day length,
84 temperature, and prey availability. *Calanus finmarchicus* has evolved its life history strategy
85 to take advantage of a relatively predictable and extended productive period, timing its
86 reproduction to match with the phytoplankton bloom (Miller et al. 1991). However, there is
87 high plasticity in the timing of overwintering and reproduction within its distributional range
88 (Johnson et al. 2008). In boreal latitudes, the overwintering period is generally shorter, lasting
89 for a couple of months, and up to three generations per year can be produced (McLaren and
90 Corkett 1986, Durbin et al. 1997, McLaren et al. 2001, Saumweber & Durbin 2006, Michaud
91 & Taggart 2007). However, populations with one-year life cycles have been described as far
92 south as the Gulf of St Lawrence and across most of the Canadian Atlantic (Plourde et al.
93 2001, Plourde et al. 2009). At the northern border of the species distributional range, *C.*
94 *finmarchicus* has a one-year life cycle (Daase et al. 2021) and the overwintering phase can last
95 for up to 10 months (Hirche 1996).

96 Overwintering depth also varies substantially across the distributional range of *C.*
97 *finmarchicus*. In the deep basins of the North Atlantic, diapause occurs in the mesopelagic layer
98 > 600 m (Heath et al. 2000). However, successful overwintering of *C. finmarchicus* populations
99 has also been observed in shallower environments such as fjords and shelf seas with bottom
100 depth typically < 300 m (Tande 1982, Hirche 1991, Durbin et al. 1995) which have a very
101 different light climate and temperature regime. Can we, therefore, expect differences in
102 behaviour and physiology between populations overwintering in environments of shallow and
103 deep bottom depth? Recent observations from the Fram Strait showed that *C. finmarchicus*
104 residing in the epipelagic at the beginning of the non-productive period were more active than
105 those residing in the mesopelagic layers (Grigor et al. 2022). Furthermore, active feeding has

106 been observed during the non-productive period in *C. finmarchicus* populations overwintering
107 in shallow environments (Butler et al. 1970, Hirche 1996) as well as during periods of limited
108 food availability such as mid-summer in the Gulf of St. Lawrence (Ohman & Runge 1994).
109 These feeding activities during periods of low food availability are usually characterized by a
110 dietary shift from herbivorous to omnivorous, carnivorous and/or detritivorous. These lines of
111 evidence suggest that populations residing in environments that are depth-constrained remain
112 more active during the non-productive period. A number of factors such as temperature, lipid
113 structure and food availability likely play a significant role causing the differences in behaviour
114 between individuals inhabiting shallow and deep environments (Pond & Tarling 2011, Pond
115 2012, Pond et al. 2014). We suggest that one of the factors preventing *C. finmarchicus* to enter
116 a classical diapause in environments with shallow water depth is the exposure to a changing
117 photoperiod, as they cannot migrate into mesopelagic layers where the absence of a changing
118 photoperiod would enable them to enter diapause.

119 Our aim was to determine locomotor activity during the overwintering period of *C.*
120 *finmarchicus* in shallow environments under ambient photoperiods at two latitudes: the boreal
121 Loch Etive (56°N, west Scotland) and the sub-Arctic Ramfjord (69°N, northern Norway). The
122 main objectives of our study were to: (1) determine if *C. finmarchicus* overwintering in shallow
123 environments enter a period of classical diapause, and (2) investigate patterns of rhythmicity
124 in swimming activity over the diel cycle at two latitudes with contrasting photoperiod.
125 Concurrently with these objectives, we characterized morphological differences between
126 boreal and sub-Arctic *C. finmarchicus* populations to determine if differences in overwintering
127 activities between these locations correlated with differences in body size and energy reserves.
128

129 **2 Method:**

130 2.1 Study area:

131 The study was conducted in Loch Etive, Scotland (UK), and in Ramfjord, near Tromsø
132 (Norway). Loch Etive is located at a boreal latitude (56°45'N, 5°18'W) (Figure 1a), where day
133 length (i.e., from sunrise to sunset) varies from ca. 7 hours in December to ca. 17 hours in June
134 (Figure 1b). Ramfjord is located north of the Arctic circle (69°31N, 19°02E) (Figure 1a).
135 Ramfjord has an Arctic light regime with the day length increasing from 0 h between the end
136 of November to the end of January (polar night) to a maximum of 24 h between the end of May
137 to end of July (midnight sun) (Figure 1b). Despite this, Ramfjord is characterized as a sub-
138 Arctic fjord since it is not directly influenced by Arctic water masses. In both locations, the
139 sampling station was located near the deepest point of the fjord, at 145 m and 130 m in Loch
140 Etive and Ramfjord, respectively.

141 2.2 Sampling

142 Monthly sampling was conducted from August 2017 to March 2018 in Loch Etive and from
143 January 2019 to December 2019 in Ramfjord (Table 1). At each sampling event, a CTD profile
144 was taken (SBE 19 in Etive, Seabird SBE 19 plus in Ramfjord, Sea-Bird electronics, Bellevue)
145 (Table 1). In Loch Etive, additional CTD profiles were taken occasionally outside of the main
146 sampling event (Table 1). *Calanus finmarchicus* was collected with a WP2 net with a closing
147 system (Hydro-Bios, Kiel) and a maximum mesh size of 200 µm. At both locations, samples
148 were taken from a few meters above the seafloor to 50 m deep and were carefully transferred
149 to the local laboratory by keeping the sampled organisms in a dark cooler to maintain stable
150 temperatures and minimizing light exposure by keeping the sampled organisms in a dark
151 cooler. Animals were transferred to a temperature-controlled room set to ambient seawater
152 temperature at the collection site and kept in these conditions overnight (about 18 h) before
153 setting up the experiments.

154 2.3 Locomotor activity

155 2.3.1 Experimental settings

156 For each location and time point, *Calanus* spp. stage five copepodites (CV) were carefully
157 picked using a stereomicroscope and soft forceps (see section 2.5 for species identification)
158 (Table1). Individual copepods (copepodite stage CV) were placed in clear uncapped acrylic
159 tubes (volume 5 ml; diameter 10 mm diameter and length 64 mm) filled with filtered seawater.
160 The sorting was performed in a temperature-controlled room in darkness but the organism were
161 exposed to light from the stereomicroscope while being sorted. To monitor the locomotor
162 activity of individual CVs, the test tubes were placed in modified LAM10 activity monitors
163 (TriKinetics, Waltham, USA). These are infrared light (IR) beam arrays which detect the
164 movement of an individual copepod in each test tube. IR beams were located at 30 mm above
165 the bottom of each tube i.e., the middle of the filled tubes. Beam breaks were registered every
166 30 seconds on a laptop computer using proprietary TriKinetics software (filescan.exe). The
167 monitors were placed in a temperature-controlled room with a controlled light environment
168 where the local ambient photoperiod was reproduced (Table 1). The light environment was
169 controlled with a LED Red Green Blue (RGB) ribbons set on white light. The light was
170 installed above the monitors (about 20/30 cm above). In Ramfjord, the individuals were
171 exposed to a day length equivalent to the time when the sun is above the horizon (real day
172 length) plus the civil twilight (the period when the sun is between the horizon and -6° below
173 the horizon) to simulate a photoperiod as close as possible to the natural light climate. Thus,
174 experiments conducted for Ramfjord during the polar night (December and January) were not
175 maintained under continuous darkness but rather under a short photoperiod (Table 1).
176 Meanwhile, individuals from Loch Etive were exposed to a day length equivalent to the time
177 between sunrise and sunset (Table 1).

178 2.3.2 Data processing

179 At the end of each experiment, the number of beam breaks for each individual was summed
180 over 30 min time bins with the DAMFileScan111 software (TriKinetics, Waltham, USA) and
181 defined as activity intensity (Act_{int}). The average activity intensity over the entire experiment,
182 called activity level (Act_{level}) was calculated for each individual. Individuals which were dead
183 at the end of the experiment (usually less than 10 %, Table 1) were removed from the data set.
184 Individuals with an $Act_{level} > 60$ breaks per 30 min were assumed to occupy a chamber with a
185 faulty sensor (based on an analysis of outliers) and likewise were removed from the data set.

186 2.4 Morphology

187 After the experiment, each individual was photographed using a stereomicroscope. The
188 resulting image was used to measure the prosome length (PL), the prosome area (PA), and the
189 lipid sac area (LA) of each individual using Image J software (Schneider et al. 2012). The lipid
190 sac area to prosome area ratio (LAPA) was calculated for each individual as an index of the
191 amount of lipids stored with each individual independent of body size (i.e., indicating lipid
192 fullness). Values are presented as means with standard deviation (mean \pm sd). Additionally,
193 LA was used to calculate the total lipid content (TL) in mg following Vogedes et al. (2010).

$$194 \quad TL = 0.197LA^{1.38} \text{ (Eq 1)}$$

195 The lipid consumption over the overwintering period (%) was calculated by deducting the
196 average LAPA during late overwintering phase from the average LAPA during early diapause.

197 2.5 Species identification

198 In Loch Etive, the *Calanus* population consists exclusively of *C. finmarchicus* (Choquet et al.
199 2017), but in Ramfjord four species of *Calanus* occur sympatrically; *C. finmarchicus*, *C.*
200 *glacialis*, *C. helgolandicus*, and *C. hyperboreus* (Coguiec et al. 2021). *Calanus hyperboreus*
201 was identified visually based on the presence of a spine on the last prosome segment but
202 molecular tools were needed to discriminate between the three other species, as they are

203 morphologically similar and overlap in size. A modified version of the Insertion-Deletion
204 markers (InDels) protocol described by Choquet et al. (2017) was therefore used to identify the
205 individuals used in the experiment in Ramfjord to species level. After the completion of the
206 experiment, DNA was extracted from individual *Calanus* using the HotShot method (Montero-
207 Pau et al. 2008). The Insertion-Deletion (InDel) molecular marker G-150 from Smolina et al.
208 (2014) was amplified by polymerase chain reaction (PCR). The resulting amplicons were
209 loaded on a 2% agarose gel and species identification was carried out based on fragment
210 lengths. The InDel marker G-150 is diagnostic to discriminate between *C. finmarchicus* and *C.*
211 *glacialis* but not *C. helgolandicus*. The abundance of *C. helgolandicus* in the fjord is very low
212 compared to other *Calanus* spp. (Coguiec et al. 2021), and in most cases, the marker G-150
213 does not amplify for that species (see dataset from Choquet et al. 2017), hence we would
214 remove individuals with no amplification from our dataset. As G-150 is not diagnostic between
215 *C. finmarchicus* and *C. helgolandicus*, there is a slight chance for a genotype identical to *C.*
216 *finmarchicus* to appear in *C. helgolandicus* for that marker. However, due to the above, we
217 consider that the likelihood of having mistakenly included *C. helgolandicus* in our dataset is
218 very low, and henceforth this is not problematic for our findings.

219 2.6 Data analysis

220 2.6.1 Processing

221 For the experiment carried out in Ramfjord, data recorded in March, April and May were
222 excluded from further analysis since not enough *C. finmarchicus* CV were present in net
223 samples (< 2 individuals per sample), which we considered not statistically representative of
224 the population.

225 A Lomb-Scargle periodogram analysis (R package lomb version 2.0) (Ruf 1999) was
226 conducted for each individual to determine whether it exhibited a rhythmic pattern in locomotor
227 activity i.e., activity response to the imposed laboratory light/dark cycle. Lomb-Scargle is a

228 particularly robust statistical analysis of rhythmic time-series data, especially for analysis of
229 marine chronobiological data (Chabot et al. 2007, Lambert et al. 2019). Its particular strength
230 lies in the analysis of unequally spaced or missing data (Ruf 1999) but it is also considered
231 equally powerful in the analysis of continuous data. Lomb-Scargle analysis is derived from the
232 principles of Bayesian probability theory and combines the strength of Fournier analysis with
233 least-square methods (VanderPlas 2018). The analysis was run for periods < 30 h. All
234 individuals that had a significant period (p-value < 0.05) were classified as rhythmic
235 individuals, while the others were categorized as arrhythmic. From this categorization the
236 percentage of rhythmicity (RH) per experiment was defined as:

$$237 \quad RH = \frac{\#rhythmic\ indiv}{\#total\ indiv} \quad (\text{Eq 2})$$

238 The rhythm strength of each rhythmic individual was defined using the peak normalized power
239 in the periodogram (PNmax) from the Lomb-Scargle analysis (Lambert et al. 2019). A higher
240 value of PNmax indicates a stronger rhythm.

241 The experiments were grouped according to overwintering phases which the animals had
242 theoretically entered at the time of the sampling, based on population dynamics and timing of
243 *C. finmarchicus* overwintering in Loch Etive (Häfker et al. 2018) and Ramfjord (Coguiec et al.
244 2021). Following Hirche (1996), we defined three overwintering phases: i) the early
245 overwintering (“early” on figures), which defines the period when part of the *C. finmarchicus*
246 CV population had descended to depth (between June and August in both locations) and is
247 equivalent to Hirche’s “induction phase”; ii) the mid-overwintering (“mid”) defined as the
248 period when the majority of the *C. finmarchicus* population was found at overwintering depth
249 (from September to November in Loch Etive, September to December in Ramfjord); equivalent
250 to Hirche’s “refractory phase”; iii) the late overwintering (“late”) defined as the time when a
251 part of the population had ascended higher up in the water column to feed and moult prior to

252 reproduction (from December to March in Loch Etive, January and February in Ramfjord), and
253 is equivalent to Hirche's "termination phase".

254 To identify differences in the timing of increased population-level activity over the diel cycle,
255 the population's daily activity was calculated as the average Act_{int} of all individuals per month
256 for each 30 min interval using data from the first three days of each experiment, thereby
257 allowing for robust chronobiological analysis whilst minimizing the impacts of prolonged
258 laboratory conditions. The data were visualized using a double-plotted actogram. For each
259 experiment, the uniformity of the daily activity over a 24 h period was tested with a Rayleigh
260 test on this daily activity data. All months in both locations showed non-uniform distributions
261 (Rayleigh test, $p < 0.05$). Accordingly, the mean angle (μ), i. e., the time around which the peak
262 of activity was centered, and the mean resultant length (ρ), i. e., the peak activity intensity,
263 were calculated for each experiment. All circular statistics were done in R with the circular
264 package (Agostinelli & Lund 2022).

265 2.6.2 Statistics

266 The normality of prosome length, LAPA, activity level, PNmax and TL were tested with a
267 Shapiro test, but none met the normality conditions ($p\text{-value} < 0.05$). The variance homogeneity
268 for each location between the different diapause phases as well as for each diapause phase
269 between the locations was tested with a Fligner test. The variances were not homogenous ($p\text{-}$
270 $value < 0.05$), except for prosome length and LAPA between each diapause phase in Loch
271 Etive ($p\text{-value} > 0.05$). Due to the absence of normality and homoscedasticity, only non-
272 parametric tests were applied.

273 For each location, the variation in prosome length, LAPA, activity level and PNmax over the
274 diapause phases was tested with a Kruskal-Wallis test. If significant ($p < 0.05$), then differences
275 among diapause phases were determined by pairwise Wilcoxon tests with a Holm's correction.

276 In addition, for LAPA and TL in Loch Etive, the effect size was calculated using Cohen d
277 method (R package effsize; Torchiano 2016).

278 For each diapause phase, prosome length, LAPA, activity level and PNmax were compared
279 between Loch Etive and Ramfjord with unilateral Wilcoxon tests.

280 All statistical tests were performed with a 5 % level of significance. All the graphs and
281 statistical tests were performed in R (version 4.01) (R Core Team 2020).

282 **3 Results**

283 3.1 Hydrography

284 In Ramfjord, during the mid-overwintering phase (September-December), surface waters
285 cooled from ~12 °C to 6 °C, decreasing gradually with depth to 5 °C at the bottom (Figure 1c).

286 Between January and May (i.e., late overwintering phase and the active period), the water
287 temperature decreased slightly from 4/5 °C to 1/2 °C. During this period the water column was
288 particularly homogenous in terms of temperature. From May the water column start to stratify
289 in terms of temperature with the surface water warmer than the bottom one. The water
290 temperature increased between May and September (early overwintering phase). In Loch Etive,
291 during the mid-overwintering phase (September-November) the water column was relatively
292 warm (12 °C) and homogenous (Figure 1d). Loch Etive had a stable water column temperature
293 below 50 m deep from July to November.

294 3.2 Morphology

295 The average prosome length of *Calanus finmarchicus* CV was higher in Ramfjord (early: 2.6
296 ± 0.1 mm, mid: 2.4 ± 0.2 mm, late: 2.3 ± 0.2 mm) than in Loch Etive (early: 2.4 ± 0.1 mm,
297 mid: 2.3 ± 0.1 mm, late: 2.3 ± 0.1 mm) during the early and mid-overwintering phase (bilateral
298 Wilcoxon p-value < 0.05), while during the late overwintering phase there was no significant
299 difference in average prosome length between Ramfjord and Loch Etive (bilateral Wilcoxon

300 test p-value = 0.18) (Figure 2a). In Ramfjord, the average prosome lengths decreased with each
301 subsequent overwintering phase (pairwise Wilcoxon p-value < 0.05, Table 2). For Loch Etive,
302 the average prosome length during early overwintering was significantly higher compared to
303 the mid-overwintering phase (pairwise Wilcoxon p-value < 0.05, Table 2). However, the
304 average prosome length was not significantly different between mid-overwintering and late
305 overwintering and between late and early overwintering (pairwise Wilcoxon p-value = 0.1071
306 and p-value = 0.1175, respectively (Table 2)).

307 The average lipid sac area to prosome area ratio (LAPA) of CVs was lower in Ramfjord (early:
308 0.25 ± 0.2 , mid: 0.49 ± 0.1 , late: 0.34 ± 0.12) than in Loch Etive (early: 0.55 ± 0.09 , mid: 0.50
309 ± 0.09 , late: 0.48 ± 0.08) during each of the overwintering phases (bilateral Wilcoxon p-value
310 < 0.05) (Figure 2b). In both locations, the average LAPA decreased in each subsequent
311 overwintering phase (Pairwise Wilcoxon p-value < 0.05 Table 2, in Loch Etive Cohen d > 0.6),
312 except for Ramfjord where the average LAPA was lowest in the early overwintering phase.
313 However, during that phase the variation in the LAPA was twice as high as during any other
314 overwintering phase in Ramfjord or Loch Etive. This large variability is caused by a low LAPA
315 in June (the lowest LAPA measured over the study period (0.16 ± 0.15)), while in August
316 (0.47 ± 0.10) the LAPA was higher and relatively close to the values measured during the other
317 overwintering phase (Figure 2c).

318 The total lipid (TL) was similar in Ramfjord (early: 0.15 mg (without June), mid: 0.14 mg) and
319 Loch Etive (early: 0.16 mg, mid: 0.12 mg) during the early and mid-overwintering phases
320 (bilateral Wilcoxon p-value > 0.05), but TL was lower in Ramfjord (0.07 mg) than in Loch Etive
321 (0.12 mg) (unilateral Wilcoxon p-value < 0.05) during the late phase. In Ramfjord, the TL
322 during the late overwintering phase was significantly lower than during the early and mid-
323 overwintering phase (pairwise Wilcoxon p-value < 0.05, Table 2) while in Loch Etive the TL

324 during the early overwintering phase was significantly higher than during the mid and late
325 overwintering phase (pairwise Wilcoxon p-value <0.05, Table 2 and Cohen d > 0.8).

326

327 3.3 Locomotor activity

328 The activity level (Act_{level}) was consistently lower in individuals from Ramfjord (early: $8.8 \pm$
329 9.7 , mid: 7.0 ± 6.0 , late: 5.1 ± 6.0) compared to individuals from Loch Etive (early: $14.7 \pm$
330 13.0 , mid: 11.1 ± 8.4 , late: 11.3 ± 9.5) (unilateral Wilcoxon tests p-value < 0.05). The average
331 activity level in Ramfjord was reduced slightly during late overwintering when compared to
332 earlier phases (Figure 3a), with significant differences observed only when compared to mid-
333 overwintering (Kruskal-Wallis p-value = 0.0009, pairwise Wilcoxon p-value < 0.05. Table 2).
334 For Loch Etive, the activity level was consistent across overwintering phases (Kruskal-Wallis
335 p-value = 0.31).

336 Rhythmic activity with a period in the circadian range (20 to 28 h) was detected in both
337 locations and for each experiment (Table 3). In Ramfjord, there was high seasonal variability
338 in the percentage of individuals expressing rhythmic swimming activity under ambient
339 temperature and photoperiod conditions, varying from 7 % in January to 82 % in August (Table
340 3). On average, 39 ± 25 % of the Ramfjord population displayed rhythmic activity. In Loch
341 Etive, the percentage of rhythmic individuals was higher and relatively stable throughout the
342 different experiments, varying from 57 % in January to 83 % in September (Table 3) and
343 averaging to 71 ± 9 % over the entire study.

344 Rhythm strength (PNmax) did not show a clear seasonal variation in Ramfjord (Figure 3b).
345 The average PNmax differed significantly between the mid and late overwintering phase
346 (pairwise Wilcoxon p-value = 0.049) while the average PNmax was not significantly different
347 between early and mid-overwintering and between late and early overwintering phase. In Loch

348 Etive, PNmax did not vary among overwintering phases (Kruskal-Wallis p-value = 0.08)
349 (Figure 3b).

350 A significant peak in activity over the diel cycle was detected for each experiment for
351 populations from both locations (Rayleigh tests p-value < 0.05). In early overwintering, a
352 nocturnal peak of activity was detected while during mid-overwintering and late overwintering
353 this peak was diurnal, in both locations. In Ramfjord, daytime peaks in activity were detected
354 between October and February. These peaks were centred over a wide range of time, 12:00 in
355 October, 14:30 in November, 10:00 in December, 14:30 in January and 13:00 in February
356 (Figure 4c). From October to December and in January the activity intensity during the peak
357 in activity was relatively low (shortest mean resultant length (ρ)) (Figure 4c). In August and
358 September, the peaks in activity happened during times when individuals were exposed to
359 darkness, with peaks centred around 01:00 in August and 00:00 in both September experiments
360 (Figure 4a & c). During these months, the activity intensity during the peak was high (longest
361 ρ) (Figure 4c). During the experiment in June, the individuals were exposed to constant
362 illumination and the peak in activity was centred around 20:00 with a relatively high activity
363 intensity over the entire 24 h period and a short mean resultant length (Figure 4a & c). In Loch
364 Etive, the peaks in activity were centred around mid-day (Figure 4d), except for July and
365 November. In July and November, the peaks in activity were observed during night-time
366 around 3:30 and 6:00, respectively (Figure 4b & d). In July, the activity intensity was relatively
367 high throughout the 24 h period. The peaks in activity were more marked during the late
368 diapause in February and March (Figure 4b & d). The shortest mean resultant length was
369 observed in October and November.

370 **4 Discussion**

371 Swimming activity of *Calanus finmarchicus* under seasonal ambient photoperiods was
372 used to characterize behaviour during the overwintering period in shallow fjords at sub-Arctic
373 and boreal latitude. We found that regardless of latitude, *C. finmarchicus* maintains diel
374 patterns of swimming activity consistent with a resting state rather than a torpid state of
375 ‘classical’ diapause as encountered in the mesopelagic (Hirche 1996, Kaartvedt 1996, Grigor
376 et al. 2022). However, at the sub-Arctic latitude the individuals were larger, less fat and less
377 active compared to the boreal latitude. The differences between the two locations and their
378 implications for *C. finmarchicus* metabolism are discussed below.

379

380 4.1 *Calanus finmarchicus*’ winter resting

381 In both Loch Etive and Ramfjord, seasonal changes in swimming activity suggest that *C.*
382 *finmarchicus* displays a different behaviour whilst overwintering in shallow fjordic
383 environments compared to a ‘classical’ diapause as observed in deep Atlantic/ Arctic off-shelf
384 waters. Grigor et al. (2022), used the LAM methodology to compare the swimming activity of
385 *C. finmarchicus* in the Fram strait from the epipelagic layer and assumed not overwintering to
386 individuals from the mesopelagic and considered as diapausing. They found that individuals
387 residing in mesopelagic layers in late August, maintain very low swimming activity (between
388 1 and 2 beam breaks 30 min⁻¹) compared to the epipelagic layer (12 to 15 breaks 30 min⁻¹).
389 While we detected peaks in activity in each experiment at both locations in the early and late
390 overwintering phases, the peak in activity throughout the mid-overwintering phase was low.
391 Since swimming accounts for 30 to 40 % of the metabolic costs in copepods (Alcaraz &
392 Strickler 1988), we interpreted the low intensity of the peak in activity during mid-
393 overwintering as a reduction in metabolism. *Calanus finmarchicus* diapause is defined as a
394 physiological state characterized by a reduced metabolism and torpidity; a definition based on

395 observations of animals from deep environments (Hirche 1996). Conversely, studies from
396 shallow environments on the eastern side of the Atlantic suggest that *C. finmarchicus* may
397 remain active during the overwintering period (Tande 1982, Hirche 1991), which is supported
398 by our observations. The activity levels measured during our study (5 to 8 breaks 30 min⁻¹ in
399 Ramfjord and 11 to 14 breaks 30 min⁻¹ in Loch Etive) are close to those reported for *C.*
400 *finmarchicus* residing in epipelagic layers (12 to 15 breaks 30 min⁻¹) in the Fram Strait in late
401 August (Grigor et al. 2022). In that study, mesopelagic *C. finmarchicus* displayed considerably
402 lower activity levels (and respiration rates) than epipelagic individuals, suggesting that the
403 mesopelagic copepods were in deep diapause (Grigor et al. 2022). Grigor et al also observed
404 higher variance in the swimming activity in the population residing in epipelagic layers (10.8
405 to 17.9) compared to those at mesopelagic layer (2.11 to 3.63), indicating higher heterogeneity
406 in the activity within the epipelagic population (some were more active than others). We
407 observed a variance close to what Grigor et al. (2022) observed in the epipelagic for all
408 overwintering phases (Ramfjord: 6 to 9, Loch Etive: 8.4 to 13). Furthermore, Grigor et al.
409 (2022) found that ~5 beam breaks 30 min⁻¹ marked the upper limit of mesopelagic activity and
410 the lower limit of epipelagic activity, which corresponds to the lowest limited found in
411 Ramfjord. These observations further strengthen our interpretation that *C. finmarchicus* in our
412 study never reached a state of diapause comparable to that observed in deep-dwelling copepods
413 by Grigor et al. (2022). It is still not fully understood what regulates the activity of
414 overwintering copepods. Freese et al. (2016) showed that the closely related *Calanus glacialis*
415 overwintering in a shallow Arctic fjord substantially reduce their digestive enzymatic activities
416 in winter, but this reduction seemed to be regulated by food availability rather than being
417 triggered by internal or behavioural factors related to overwintering. The term “active
418 diapause” has previously been used for other copepod species such as *Acartia longiremis* and
419 *Pseudocalanus acuspes* to describe a state where metabolism is reduced but the organisms

420 remain partially active (Corner et al. 1974, Elgmork 1980, Williams & Conway 1982, Williams
421 & Conway 1984, Næss & Nilssen 1991, Norrbin 1996, Svetlichny et al. 1998, Grigor et al.
422 2022). Since diapause is generally described as a phase of dormancy with delayed development
423 and reduced metabolic activity, the term “active” diapause is somewhat contradictory, and
424 instead, we suggest describing the state of overwintering *C. finmarchicus* in shallow
425 environments as entering a “winter resting” state.

426 During the winter resting phase, rhythmicity in the population in response to ambient
427 photoperiods was overall lower, the rhythms in activity were weaker, and the individuals were
428 less active at the sub-Arctic latitude than at the boreal location. Furthermore, the activity level
429 remained constant during winter resting in Loch Etive, while in Ramfjord the animals became
430 less active during the late overwintering phase. In flies, temperature and photoperiod have been
431 described as factors with an important influence on flying, with high temperatures resulting in
432 more flight and increased rhythmicity while both long and short photoperiods induce lower
433 rhythmicity (Kauranen et al. 2012, Kauranen et al. 2016). It has been suggested that these
434 factors synergically impact the flying activity of flies, with a combination of temperature and
435 photoperiod supporting a more robust rhythm and higher activity level (Kauranen et al. 2012,
436 Kauranen et al. 2016). We suggest that for *C. finmarchicus* the photoperiod and temperature
437 conditions encountered in Loch Etive facilitate increased and rhythmic swimming behaviour.

438

439 4.2 *Calanus finmarchicus*’ seasonal response to photoperiod

440 Photoperiodic responses were characterized by the appearance of peaks in activity
441 coincident with either the light or dark phase of the laboratory diel cycle i.e., day or night. We
442 hypothesize that the response to light is a negative phototactic reaction (Miljeteig et al. 2014)
443 with the individual increasing the number of beam breaks as it moves throughout the tube trying
444 to escape the light (Miljeteig et al. 2014). However, this hypothesis does not explain the

445 behaviour observed in individuals from Ramfjord during the June experiment, when the
446 individuals were exposed to constant illumination and nevertheless showed a distinct peak in
447 activity in the population. The maintenance of an activity rhythm under constant light
448 conditions in the absence of any other environmental cue is a sign that the internal clock can
449 entrain a rhythm, which has been demonstrated in *C. finmarchicus* (Häefker et al. 2017). Such
450 endogenous rhythms are commonly observed in locomotor activity studies (Bregazzi & Naylor
451 1972, Sánchez-Vázquez & Tabata 1998), particularly in flies, which can maintain rhythms for
452 weeks under constant environmental conditions (Dubruille & Emery 2008). However, in
453 terrestrial environments constant illumination is also associated with a decrease or an absence
454 of rhythmicity (Van Oort et al. 2005, Kauranen et al. 2012, Menegazzi et al. 2017, Beauchamp
455 et al. 2018, Bertolini et al. 2019). In Ramfjord during mid-summer, under constant
456 illumination, only 8% of the population was rhythmic, one of the lowest rhythmicity
457 percentages recorded over the entire study. This low percentage of rhythmic individuals
458 indicates that a peak in activity is only present in a low proportion of the studied individuals
459 while the majority of the population did not show a peak in activity. It is likely that *C.*
460 *finmarchicus*, like many marine organisms (Naylor 2010), cannot maintain rhythmic activity
461 for a long time in absence of environmental cues (Häferker et al. 2017). In its natural environment
462 in Ramfjord, *C. finmarchicus* is exposed to daily variations in light intensity and spectral
463 quality, despite the presence of midnight sun, due to diel shift in the sun altitude above the
464 horizon and the light attenuation in the water column (Miller et al. 1991, Cohen et al. 2020).
465 Thus, we hypothesize that *C. finmarchicus* did possess a functional biological clock prior to
466 the experiment (Häferker et al. 2017), but the overt absence of environmental cues during the
467 experiment led to the rapid loss of the rhythm. The peak of activity during night in August and
468 September in Ramfjord and July and November in Loch Etive remains unexplained. Under
469 natural conditions, such a behaviour could indicate active feeding during nighttime, which *a*

470 *priori* differs between summer, when more food is available than during the overwintering
471 period. However, as our experiments were conducted without food supplied, we are not able to
472 conclude if this behaviour reflects feeding activity. Furthermore, physiological difference (such
473 as change in metabolic rate) may also be involved in this behaviour. Based on our experiments
474 we are not able to explain this peak in activity during night time and additional studies are
475 needed testing multiple factors (such as food concentration, temperature changes, predator
476 presences) that could evoke this behaviour.

477

478 4.3 *Calanus finmarchicus* ' morphology

479 While we found differences in body size and lipid content between the two study sites,
480 these were most likely related to differences in temperature and food availability, rather than
481 photoperiod. However, seasonal changes in the morphological parameters provide some
482 insights into the seasonal changes in activity. We show that body size (i.e., prosome length)
483 was within ranges previously reported for *C. finmarchicus* CV in similar environments as our
484 sampling locations, e.g., Disko Bay (Madsen et al. 2001) and Georges Bank (Miller et al.,
485 2000). Overall, the individuals from Ramfjord were bigger but had proportionally smaller lipid
486 reserves than the individuals from Loch Etive. *Calanus finmarchicus* growth is temperature
487 dependant. Low temperature favour long development time and an investment in reserve
488 accumulation rather than fast turnover, while at higher temperature, short development time
489 and fast turnover are stimulated. This leads to *C. finmarchicus* individual to be bigger with
490 higher lipid reserve at high temperature than at high temperature (Huntley & Lopez 1992,
491 Campbell et al. 2001, Møller et al. 2012). We suggest that this temperature dependency of *C.*
492 *finmarchicus*, may explain these size differences.

493 Since low temperatures lead to a longer development time and a higher investment in
494 reserve building it was expected for *C. finmarchicus* in Ramfjord to have more lipid reserve

495 than in Loch Etive (Pepin & Head 2009). However, we observed a lower LAPA in Ramfjord
496 with an amount of lipid similar to Loch Etive indicating that *C. finmarchicus* did not
497 accumulate more lipid than in Loch Etive as expected. Furthermore, a higher loss of lipid was
498 observed in Ramfjord with a loss of 27 % of the lipid reserves and 12 % in Loch Etive. In
499 Ramfjord, the LAPA and total amount of lipid was lower during the early overwintering phase
500 compared to the other overwintering phase because of the low LAPA and total lipid content in
501 June. We concluded that most CVs individuals did not accumulate enough lipid in June and
502 were probably not yet ready to overwinter despite residing at depth. Consequently, we excluded
503 June from the early overwintering phase when calculating the lipid consumption over the
504 overwintering period. Overall, we see a clear decrease in lipid content over the overwintering
505 period (August-February) in both locations. This loss of lipid throughout the overwintering
506 period is in agreement with previous studies showing high lipid consumption during
507 overwintering in shallow environments (e.g., 50 % of the lipid reserve), as compared to the
508 limited lipid consumption during diapause in deeper environments (5 % of the lipid reserve)
509 (Jónasdóttir 1999, Campbell et al. 2004, Clark et al. 2012). An important loss of lipid during
510 the overwintering has also been reported in deep environment on the in the Labrador Sea (Pepin
511 & Head 2009). We suggest that the more marked lipid decrease in Ramfjord compared to Loch
512 Etive is the result of more active feeding activity during overwintering in Loch Etive compared
513 to Ramfjord and/or a higher consumption of lipid in Ramfjord. The light cycle at high latitudes
514 constrains primary production. At boreal latitudes, light may reduce the primary productivity
515 during autumn and winter, but under favourable nutrient conditions, elevated primary
516 production is possible year-round (Wood et al. 1973, Brand 2018). Furthermore, Loch Etive
517 has considerable suspended organic matter (Ansell 1974, Brand 2018), which could enhance
518 *C. finmarchicus* feeding activity during overwintering as this species can switch its dietary
519 preferences i.e., to detritivory when preferred food items become scarce (Marshall & Orr 1958,

520 Butler et al. 1970, Corner et al. 1974, Ohman & Runge 1994, Hirche 1996). The larger body
521 sizes observed in Ramfjord are energetically more costly in terms of maintenance (Saumweber
522 & Durbin 2006) and could explain a higher consumption of lipid than in Loch Etive. However,
523 in Loch Etive the individuals are also subject to high lipid consumption due to the high
524 temperature of their environment. Consequently, it is impossible to establish if lipid
525 consumption is higher in Ramfjord than in Loch Etive with the data collected in this study. A
526 more detailed energetic budget would be necessary to do so. The combination of lipid
527 consumption rate and food availability explain both the counter-intuitive higher lipid fullness
528 at boreal latitudes and the higher activity level. In summary, at boreal latitudes, more energy
529 can be allocated to swimming activity and larger lipid reserve can be accumulated, due to better
530 availability of food resources and possibly reduced costs of metabolic maintenance.

531 *Calanus finmarchicus* CV body size decreased progressively through the overwintering
532 period in sub-Arctic latitudes but not at boreal latitudes. The production of a second generation
533 has previously been suggested for the population in Ramfjord, with a first generation being
534 produced around the spring bloom (i.e., April/May) and the second one in early autumn
535 (Coguiec et al. 2021). Since *C. finmarchicus* growth is temperature dependent (Huntley &
536 Lopez 1992, Campbell et al. 2001, Møller et al. 2012), and the surface water is warming from
537 late spring, the ontogenetic development of the second generation is shorter than that of the
538 first generation, which could result in animals with a smaller body size entering the
539 overwintering population later in the season. This could explain the decrease in average
540 prosome length in Ramfjord, especially between the early and mid-diapause phases. A
541 difference in prosome length between two generations of the same population due to
542 differences in surface water temperature has previously been described for the Newfoundland
543 continental shelf and the Labrador Sea (Pepin & Head 2009). The advection of the second
544 generation in Ramfjord from Atlantic water can similarly explain the decrease in prosome

545 length. Advection in Ramfjord has previously been reported at the time of the mid-
546 overwintering period (Coguiec et al. 2021). Changes in average prosome length during
547 overwintering can also be explained by early moulting of the bigger individuals to adults.
548 Kosobokova (1998) found that during autumn/winter in the White Sea *Calanus glacialis* males
549 derive from larger CV individuals and appear earlier than females in the population, and such
550 mechanisms would lead to a decrease in prosome length of the CVs' population. Finally, we
551 cannot exclude that a seasonal change in predation pressure on larger individuals may have
552 pushed the population towards smaller body sizes. In Loch Etive, it has been shown that *C.*
553 *finmarchicus* produces a single generation (Hill 2009, Clark et al. 2012) but a more recent study
554 found two generations in Loch Etive and suggest that the nutrient enrichment due to fish
555 aquaculture might explain the transition to two-generation a year population dynamics (Häfker
556 et al. 2018). Our prosome length data do not indicate a change in the population size structure
557 that may indicate the appearance of a second generation. However, given the rather stable water
558 surface temperature during spring and winter in Loch Etive, a second generation may not
559 necessarily be characterized by a difference in prosome length and would therefore not be
560 detectable as a change in average prosome length.

561

562 4.4 Methodological consideration

563 A disturbance of the diapause state due to rapid changes in pressure, temperature and light
564 during sampling as well as due to the light exposure during sorting is a concern with the method
565 we used. To keep light exposure at a minimum, the sampled organisms were transfer to a
566 container immediately after collection which was sealed at once, and the organisms were kept
567 in darkness until the start of the sorting. During the sorting, the room was maintained dark but
568 organisms were expose to the light emitted by the stereomicroscope. However, Miller et al.
569 (1991) demonstrated that following an exposure that triggered the diapause exit, a minimum

570 of 10 days were needed to reverse the diapause state. Thus, we find it unlikely that sampling
571 and setting up the experiments has severely disturbed the diapause state. We are convinced that
572 our method is suitable to detect diapause/ overwintering, especially since the focus is on a
573 comparison with non-overwintering individuals, either looking at seasonal variability (this
574 study) or spatial variability (Grigor et al. 2022). But swimming activity as an indicator of
575 overwintering and/or diapause is mainly applicable on population level, while characterizing
576 the mechanism of diapause at the individual level remains a challenge. This limitation
577 complicates the investigation of the associated physiological processes, particularly for
578 populations inhabiting shallow environments as the metabolism reduction is not as marked as
579 in deeper environments. The development of molecular marker to identify diapause and winter
580 resting is essential to increase the understanding of the physiological process behind
581 overwintering (Tarrant et al. 2016, Skottene et al. 2019, Lenz et al. 2021).

582

583 **5 Conclusion**

584 This study helps improve the definition of the overwintering period in *C. finmarchicus* as a
585 gradient in behaviour and physiology. It provides additional evidence towards the adaptability
586 of *C. finmarchicus* to local environments (Tarling et al. 2022a) and may have implications for
587 *C. finmarchicus* in a future warmer world, specifically winter survival, since increased
588 swimming activity may deplete lipid reserves faster (Tarling et al. 2022b). This adaptability
589 may be constrained where and when winter food supplies are restricted. Indeed, high winter
590 mortality in shallow environments in Svalbard in both *C. finmarchicus* and *C. glacialis* have
591 been attributed to insufficient energy stores to sustain activities throughout winter (Daase &
592 Søreide 2021). However, our observations from Loch Etive suggest that elevated food
593 availability throughout winter allows for sustained activity and less dependence on lipid
594 reserves, supporting a recent model study which showed that exiting diapause early does not

595 lead to poorer fitness as long as food is available (Hobbs et al. 2020). It will now be important
596 to determine how elevated swimming activity during overwintering may affect the energy
597 budget of *C. finmarchicus* in predicting how climate warming may affect their fitness during
598 overwintering. Finally, a gradient in swimming activity of overwintering copepods provides an
599 opportunity for molecular studies to elucidate fundamental processes in diapause by
600 characterizing different overwintering phenotypes in relation to genotype.

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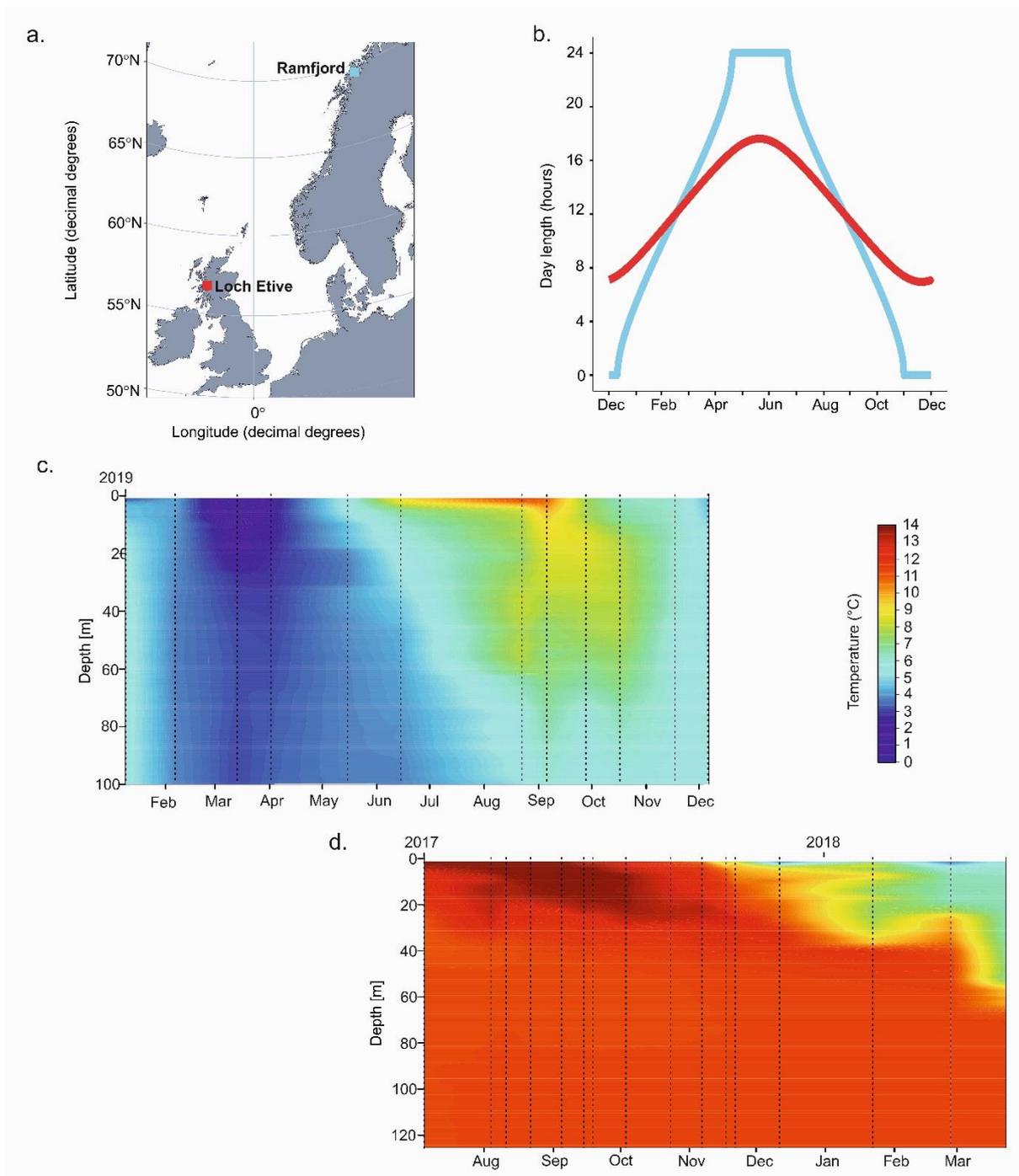
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857 **8 Figures**



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Figure 1: Map of the sampling station locations (a) and day length curve (b), temperature contour plot in Ramfjord (c) from January 2019 to December 2019 and Loch Etive (d.) from July 2017 to March 2018. The black dotted lines in the contour plots are showing the time of the CTD profile collection.

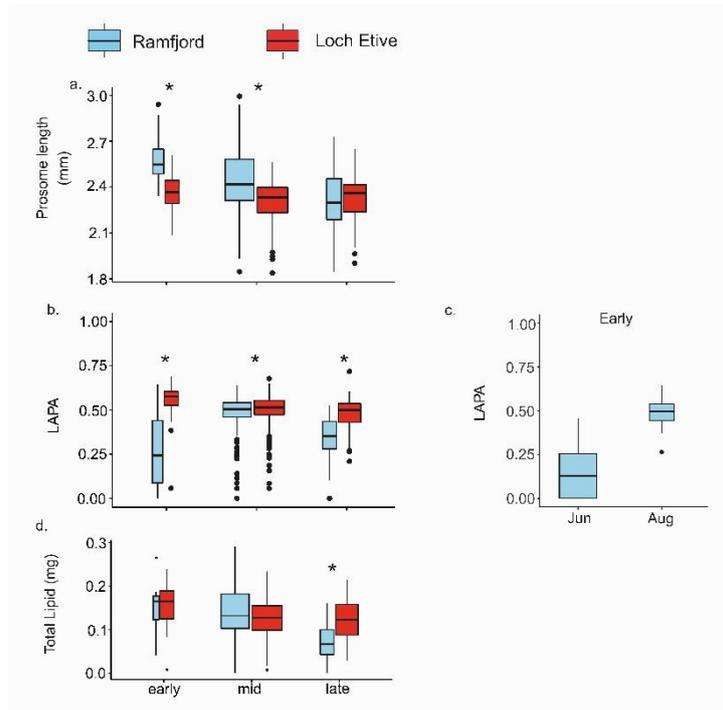


Figure 2: Variation in prosome length (a.), lipid sac area to prosome area ratio (LAPA) (b.) and total amount of lipid in mg (d) of *Calanus finmarchicus* CV during the different overwintering phases in Ramfjord (blue) and Loch Etive (red) and variation of the LAPA during the early overwintering in Ramfjord (c.). The early Total Lipid values do not include measurements from June, but June is included for the prosome length and LAPA. The asterisks indicate when the variable is significantly different between Ramfjord and Loch Etive for a given phase. The width of each box is proportional to the number of individuals used during each diapause phase. The p-value of the pairwise Wilcoxon test are presented in Table 2

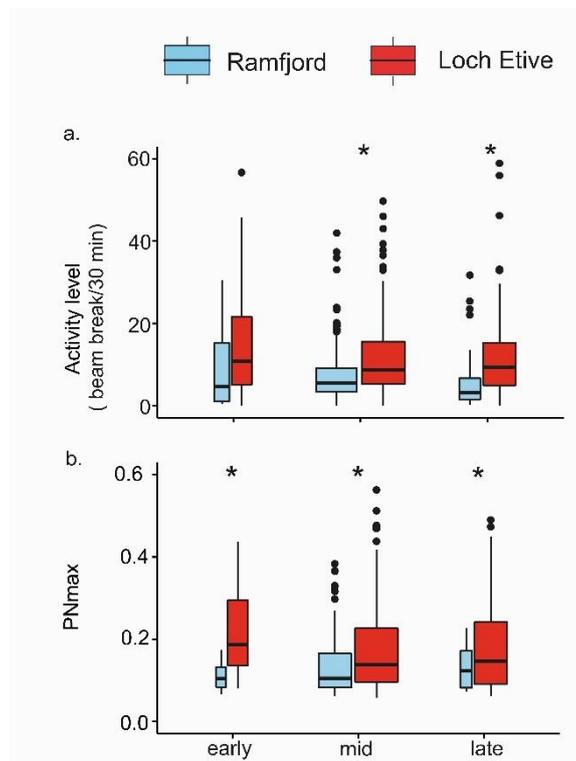
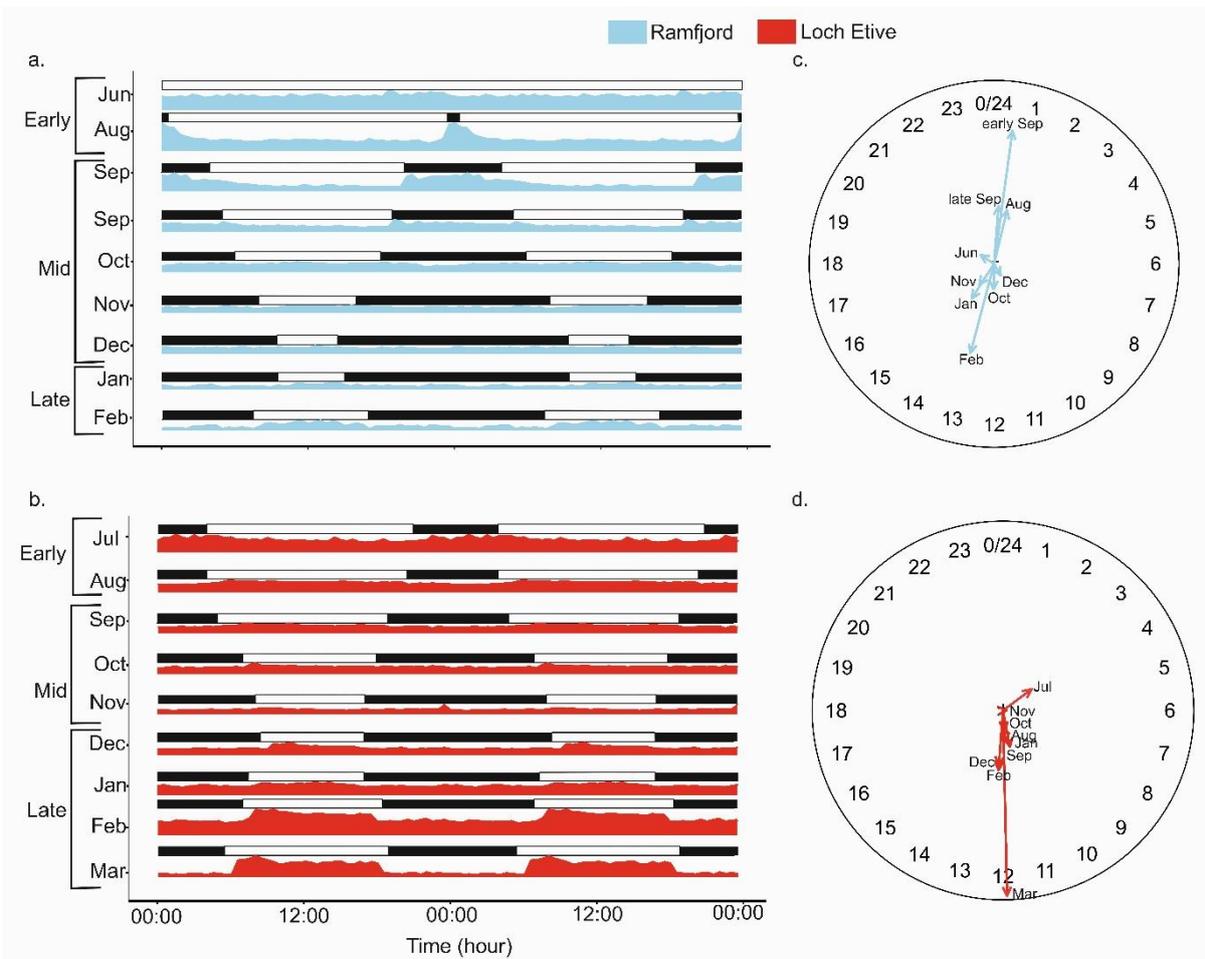


Figure 3: Variation in activity level (beam break/30min) (a.), peak normalized power (PNmax) (b.) of *Calanus finmarchicus* CV during different overwintering phases in Ramfjord (blue) and Loch Etive (red). The asterisks indicate when the variable is significantly different between Ramfjord and Loch Etive for a given phase. The width of each box is proportional to the number of individuals used during each overwintering phase. The p-value of the pairwise Wilcoxon test are presented in Table 2.



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 864 *Figure 4: Actogram of the daily activity (left panels) and the mean angle (μ) and mean resultant length (ρ) (right panel) of the*
 865 *daily activity over the 3 first days of the experiment obtained by combining all the individuals sampled during each month in*
 866 *Ramfjord (a & c) and Loch Etive (b & d). For the actogram, the 24 hours were doubled and joined to have better visualisation*
 867 *during the night time. The black segments on top of each actogram, indicate the period when the light was off. The*
 868 *overwintering phases corresponding to the month are indicated on the left side of the y-axis. All months had non-uniform*
 869 *circular distributions (Rayleigh test $p < 0.05$). Mean angles correspond to the time of day for peak activity in a given month,*
 870 *with the mean resultant length (plotted here as $\rho * 2.5$, for clarity) corresponding to the strength of that activity. Months are*
 871 *labelled for each mean vector.*

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Table 1: Overview of the sampling events, experiment setting and composition of each experiment. The light cycle format indicates the number of hours of light per day: the number of hours of darkness per day. The number of Calanus correspond to the number of individuals used in the experiment, the number of CV indicate how many of these were stage CV. From this CV the number of were dead, Calanus finmarchicus, Calanus glacialis and unknown is indicated in the following column

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Location	Date	CTD	Nets	Experiment duration	Light cycle	Number Calanus sampled	Number Calanus CV	Number Calanus dead	C. fin	C. gla	Unknown
Ramfjord	09/01/2019	x	x	4d	4.5 L : 19.5 D	64	54	5	43	5	1
	06/02/2019	x	x	6d	8.5 L : 15.5 D	64	36	7	27	0	2
	13/03/2019	x	x	6d	13.5 L : 10.5 D	32	1	0	1	0	0
	01/04/2019	x	x	6d	17 L : 7 D	30	4	0	2	2	0
	14/04/2019	x	x	5d	19 L : 5 D	50	2	0	0	2	0
	14/05/2019	x	x	4d	24 L : 0 D	32	10	0	0	10	0
	13/06/2019	x	x	6d	24 L : 0 D	64	52	0	26	25	1
	20/08/2019	x	x	7d	22 L : 2 D	64	50	10	11	28	1
	03/09/2019	x	x	7d	15 L : 9 D	122	92	3	30	24	35
	25/09/2019	x	x	7d	13 L : 11 D	96	78	1	50	23	4
	14/10/2019	x	x	6d	11 L : 13 D	128	117	1	60	51	5
	14/11/2019	x	x	5d	7 L : 17 D	128	108	2	50	56	0
03/12/2019	x	x	6d	4 L : 20 D	116	100	0	72	23	5	
Loch Etive	04/07/2017		x	5d	16 L : 8 D	94	89	23	65	-	-
	11/07/2017	x				-	-	-	-	-	-
	03/08/2017	x				-	-	-	-	-	-
	10/08/2017	x				-	-	-	-	-	-
	21/08/2017	x				-	-	-	-	-	-
	23/08/2017			x	5d	14.5 L : 9.5 D	93	87	3	83	-

04/09/2017	x				-	-	-	-	-	-
14/09/2017	x				-	-	-	-	-	-
18/09/2017	x	x	5d	13 L : 11 D	96	80	0	80	-	-
03/10/2017	x				-	-	-	-	-	-
23/10/2017	x	x	6d	10 L : 14 D	96	67	1	67	-	-
06/11/2017	x				-	-	-	-	-	-
17/11/2017	x				-	-	-	-	-	-
21/11/2017	x	x	8d	8 L : 16 D	96	79	0	79	-	-
27/11/2017	x				-	-	-	-	-	-
11/12/2017	x	x	6d	7.5 L : 16.5 D	96	88	1	87	-	-
22/01/2018	x	x	6d	8.5 L : 15.5 D	96	95	32	63	-	-
26/02/2018	x	x	6d	10.5 L : 13.5D	96	19	0	19	-	-
23/03/2018	x	x	5d	12.5 L : 11.5 D	96	7	0	7	-	-

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884 Table 2: Table summarizing the p-value of the pairwise Wilcoxon test comparing the variable (prosome length, LAPA, total
 885 lipid, Activity level and PNmax) over the overwintering phase for each location. The bold and underlined numbers indicate a
 886 significant difference.

		Ramfjord		Loch Etive	
		Early	Mid	Early	Mid
Prosome Length	Mid	<u>0.0001</u>	-	<u>0.0059</u>	-
	Late	<u>1.10E-09</u>	<u>4.40E-06</u>	0.1175	0.1071
LAPA	Mid	<u>1.30E-10</u>	-	<u>6.10E-09</u>	-
	Late	<u>0.043</u>	<u>< 2e-16</u>	<u>1.90E-11</u>	<u>0.0022</u>
Total Lipid	Mid	0.38613	-	<u>3.60E-07</u>	-
	Late	<u>0.00019</u>	<u>5.40E-15</u>	<u>8.60E-07</u>	0.65
Activity level	Mid	0.92	-	0.42	-
	Late	0.92	<u>0.0003</u>	0.42	0.99
PNmax	Mid	0.049	-	0.11	-
	Late	0.065	0.499	0.11	0.67

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888 Table 3: Percentage of rhythmicity for each experiment.

	Jan	Feb	Mar	Jun	Jul	Aug	early Sep	late Sep	Oct	Nov	Dec
Ramfjord	6.98	44.4		8		81.8	63.8	68	44.1	32	36.1
Loch Etive	69	78.6	57.1		75	65.1		83.5	81.8	59.4	77

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